



Coastal palaeoenvironments and hunter-gatherer plant-use at Waterfall Bluff rock shelter in Mpondoland (South Africa) from MIS 3 to the Early Holocene

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ABSTRACT

Waterfall Bluff, in Eastern Mpondoland (Eastern Cape Province, South Africa), is a recently excavated archaeological site with deposits spanning Marine Isotope Stage (MIS) 3 to the Middle Holocene. Here, we present preliminary results of a multi-proxy palaeoenvironmental study combining macro-botanical remains, charcoal, phytoliths, pollen and plant waxes derived from the same archaeological record. We aim to understand the interactions between hunter-gatherer plant foraging and climate and environmental change in coastal Mpondoland from MIS 3 to the Early Holocene at Waterfall Bluff. The charcoal and pollen records at Waterfall Bluff show the gathering of a variety of woody taxa characterised by their combustion and medicinal properties (e.g., *Millettia grandis* and *Apodytes dimidiata*). The leaves identified in the macrobotanics and in the phytolith record might belong to some of these taxa and it is likely that they were used for medicinal purposes. From a palaeoenvironmental perspective, our results indicate low precipitation and low rainfall seasonality under cool conditions during MIS 3 and the Last Glacial Maximum (LGM). Under these conditions, open woodlands interspersed with dry and hygrophilous grasslands and bushveld vegetation with significant representation of fynbos elements occurred in the local landscapes probably along *Podocarpus/Afrocarpus* forests. The latter could have been (1) present along river valleys and scarps on the Mpondoland exposed continental shelf towards the south and west of Waterfall Bluff, supported by palaeo-rivers and cool temperatures favouring low evapotranspiration, or (2) present in the interior with pollen grains possibly transported to the site by intensified westerly winds. These forests contracted as a result of the post-glacial marine transgression or reduced westerlies following the LGM. During the Early Holocene, the palaeoenvironmental signal points to higher summer rainfall and higher (summer) seasonality than during MIS 3, the LGM and the LGIT. These changes are coeval with an increase of coastal forests and C₄ mesic grasslands with localized wetland vegetation around Waterfall Bluff. These multi-proxy archaeobotanical and biochemical data show that landscapes surrounding Waterfall Bluff changed in relation to marine transgressions/regressions and changes in rainfall intensity and seasonality. The people of Waterfall Bluff foraged the coasts during glacial periods to collect wood.

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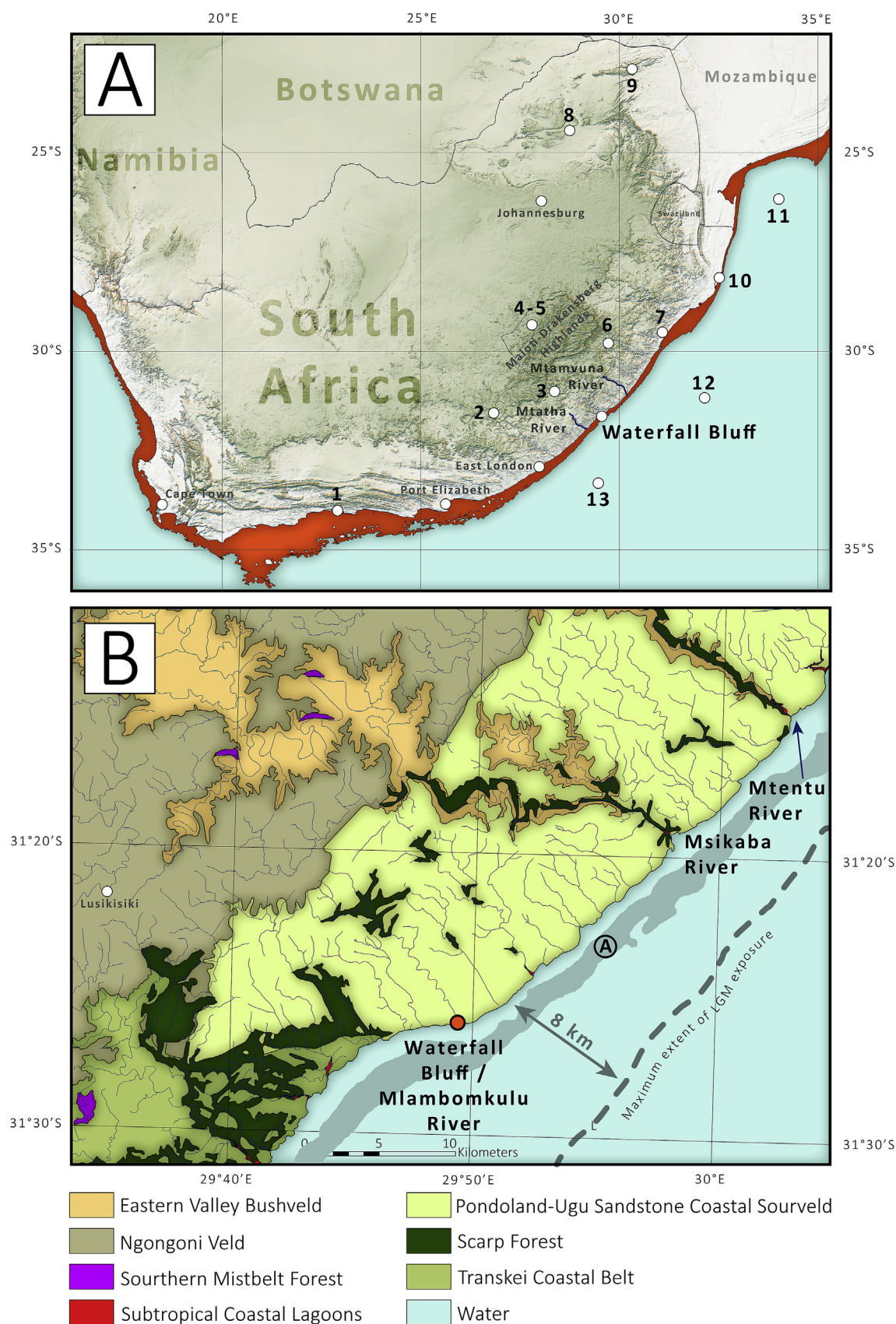


Fig. 1. The palaeoenvironmental and vegetation context of Waterfall Bluff rock shelter. A, Map of the study area showing the location of Waterfall Bluff rock shelter, the Mthatha and Mtamvuna rivers, and other relevant palaeoenvironmental records referenced in the text. The maximum exposure of the continental shelf during the last glacial maximum is indicated in orange. 1, Vankersvlei; 2, Grassridge; 3, Strathlahan B; 4, Ntloan Tsoana; 5, Ha Makototo; 6, Mahaqwa S; 7, Sibudu; 8, Wonderkrater; 9, Tate Vondo; 10, Mfabeni; 11, MD96-2048; 12, CD154-10-06 P; 13, CD154-17-17 K. B, Detailed map of the major vegetation types occurring in the study region after Mucina and Rutherford (2006),

1. Introduction

Climatic and environmental changes across the Pleistocene's glacial and interglacial phases globally shifted the habitats and, ultimately, the availability of plant, animal, and freshwater resources on which hunter-gatherers depended (e.g., Kelly, 1995; Marean, 2010; Marean et al., 2015). The record of how those people adapted over time is preserved in archaeological material culture and to interpret these records archaeologists frequently consult ethnographic records of modern hunter-gatherers to develop models of their behaviour under varying circumstances. Unfortunately, contemporary hunter-gatherer groups in Africa are largely limited to marginal environments where resource availability and predictability are low. The behavioural models derived from studies of hunter-gatherers living in these kinds of environments therefore offer limited comparison to hunter-gatherers that may have lived in different kinds of environments, like coastlines.

What makes coastlines so different is that these places provide natural buffers against the effects of localized resource instability triggered by climatic and environmental variability. This is because coastal zones frequently experience moderate climates and support diverse marine and terrestrial ecologies not found inland (Compton, 2011; Jerardino, 2010; Marean, 2010; Marean et al., 2007; Parkington, 2003; Will et al., 2016). In South Africa, which is far-field with respect to the ice sheets and generally experiences glacio-eustatic sea-level change (e.g., Carr et al., 2010; Cawthra et al., 2018; Roberts et al., 2012) evidence for coastal foraging is nearly absent on account of sea level-rise, submergence of the continental shelf, and the subsequent loss of shelf habitat (e.g., Marean et al., 2020). Across southern Africa, there are few places with narrow and steep continental margins that restrict coastline movements and that promote relative coastal stability. Mpondoland, on South Africa's remote Indian Ocean coastline, is one of those places (Fig. 1). It has a narrow continental shelf that is only ~8 km wide, meaning that sites on the modern coastline would have still been within daily coastal foraging ranges of hunter-gatherers during glacial phases (Fisher et al., 2013, 2020). The region also has coastal caves and rock shelters that preserve rich archaeological records (Chubb et al., 1934; Fisher et al., 2013), abundant rivers for fresh water, alongside high plant (Myers et al., 2000; van Wyk, 1990, 1994) and animal biodiversity (Hayward et al., 2005; Perera et al., 2011).

Fisher et al. (2013) hypothesised that Mpondoland preserves records of coastal foraging spanning both glacial and interglacial phases because of its narrow continental shelf. Excavations at the coastal Waterfall Bluff rock shelter in the Lambisa area of Eastern Mpondoland have revealed archaeological deposits dated to five main time periods (see Fig. 6 in Fisher et al., 2020): Marine Isotope Stage (MIS) 3 (ca. 39–29 ka); the Last Glacial Maximum (LGM; ca. 26.5–19 ka); the last glacial/interglacial transition (LGIT; ca. 17 ka – 11.7 ka); the Early Holocene (11.7 – ca. 8 ka) and the Middle Holocene (ca. 8–5 ka). Importantly, the deposits also preserve the first direct evidence of coastal foraging during a glacial maximum and across a glacial/interglacial transition (Fisher et al., 2020). This confirmation of persistent coastal ecosystem exploitation during the Quaternary makes Waterfall Bluff an ideal site for studying hunter-gatherer's use of plants and resource availability and its coupled response to climate and environmental changes.

Here, we use an integrative approach of biotic and abiotic indicators (charcoal, macro-plant remains, phytoliths, pollen and

plant wax carbon and hydrogen isotope compositions) to reconstruct plant gathering strategies and palaeoenvironments. Macrobotanical remains, including charcoal, provide valuable information on human behaviors related to harvesting strategies, exploitation of plant resources and use of fire. Furthermore, since trees are environmentally sensitive, the taxa identified in the preserved macrobotanical records can also inform on local and regional environmental conditions (e.g., Reitz and Shackley, 2012). Archaeological phytolith assemblages have been mainly used to provide information on wood-fuel and hearth function, plant gathering strategies and domestication (e.g., Cabanes, 2020). However, they can also be used to infer past plant availability and environmental conditions of the local environments (e.g., Cabanes, 2020). Airborne pollen can be deposited in archaeological rock shelters in relation to prevailing wind directions, and when preserved, it can be a good representative of local and/or regional environments (Carrión and Scott, 1999). On the other hand, pollen and spores can also become part of the archaeological record through human activities by introducing large amounts of plant material including pollen (Bryant and Holloway, 1996). Long-chain *n*-alkanes from plant-waxes can be used to assess plant types (i.e., woody plants vs grasses and succulents; Carr et al., 2014; Diefendorf and Freimuth, 2017; Vogts et al., 2009). Their isotopic compositions provide information on pathways of carbon fixation in plants ($\delta^{13}\text{C}_{\text{wax}}$; $\text{C}_3/\text{C}_4/\text{CAM}$; e.g., Diefendorf and Freimuth, 2017) and changes in the isotopic composition of the water used during lipid biosynthesis ($\delta\text{D}_{\text{wax}}$; Sachse et al., 2012).

This paper presents initial results of these proxy studies conducted on a vertical stratigraphic section at Waterfall Bluff, which covers the time frame from MIS 3 to the Early Holocene and includes deposits dated to the LGM and LGIT (Table 1; Fisher et al., 2020). We aim to reconstruct 1) how the coastal plain, hinterland, and each area's natural resources were influenced by climatic and environmental changes and marine transgressions/regressions, and 2) how these changes shaped the crucial plant resources that would have attracted hunter-gatherers to the Mpondoland coast from MIS 3 to the Holocene.

2. Study area

2.1. Site background

Waterfall Bluff rock shelter is located adjacent to the Mlam-bomkulu River which terminates in a ~60 m high waterfall flowing into the Indian Ocean (Figs. 1 and 2; 31°26'01, 1''S, 29°49'19.2''E). Excavations in 2015, 2016 and 2019 revealed a well-preserved stratigraphic sequence that has been subdivided into two main phases (Fisher et al., 2020), called "Stratigraphic Aggregates" (hereafter, StratAgg), which are then subdivided into sub-Stratigraphic Aggregates (hereafter, SubAggs), representing identifiable and discrete anthropogenic, biogenic, or geologic events. The earliest StratAgg is called the Light Brown Coarse Sands (LBCS), whose oldest deposits have been dated via single-grain optically stimulated luminescence (OSL) to 37.6 ± 4.2 ka. The youngest LBCS deposits have been dated via OSL to 12.5 ± 1.2 ka (minimum age of sediment deposition) and Bayesian ^{14}C accelerator mass spectrometry model from 13,520–12,830 cal yr BP to 14,070–13,570 cal yr BP (Table 1; see Table 3 and 4 in Fisher et al., 2020). Overlying the LBCS are the Shell Rich Clayey Sands (SRCS) StratAgg, which have been dated using Bayesian ^{14}C accelerator

indicating the location of Waterfall Bluff and major rivers (Mlam-bomkulu, Msikaba and Mntentu). The grey bar (A) demarcates the coastlines at 3 and 1.5 km away from Waterfall Bluff. Distance of the coastline from the site during the last glacial maximum is also given. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Sediment samples analysed for thei phytoliths, pollen and leaf wax composition. List of the thirty-three sediment samples used in this study giving sample's number, their stratigraphic provenance and depth, ages and sedimentological character of the deposits. Sediment colour follows the Munsell Colour Chart. Modelled radiocarbon ages are based on Bayesian Modeling using Oxcal 4.3 (Ramsey, 2009). Bayesian model results are reported at the 68% confidence interval and full results and data are provided in Fisher et al. (2020).

Sample Numbers	Stratigraphic Aggregate (StratAgg)	Sub-Aggregate (SubAgg)	Depth Below Surface (meters)	Modelled Radiocarbon Ages (cal yr BP) OSL Ages	Sediment description
Pollen Phytolith Leaf wax					
271 272 273	SRCS	Jess	0.06	10,750–10,720 to 10,770 –10,730	Dense layer of well-preserved <i>Perna perna</i> shells in a shell-supported matrix. 7.5 YR 4/2 Brown.
274 275 276	SRCS	Jess	0.17	10,750–10,720 to 10,770 –10,730	Stratified charcoal and ash-rich sands. 7.5 YR 4/2 Brown.
277 278 279	SRCS	Rosa	0.26	–	Banded dark red sand. 7.5 R 2.5/3 Very dusky red.
280 283 284	SRCS	West	0.29	–	Ash rich sediments with several well-preserved combustion features. 2.5 YR 3/2 Dark olive grey.
285 286 287	SRCS	Courtney	0.33	11,060–10,990 to 11,160 –11,050	Stacked and cross-bedded combustion features. 2.5 YR 2.5/5 Dark reddish brown.
288 289 290	LBCS	Kuka	0.41	13.3 ± 0.7 ka 13,520–12,830 to 14,070 –13,570	Very coarse, loosely-compacted sand with sub-rounded grains. 10 YR 4/3 Olive Brown.
292 293 291	LBCS	Lily	0.48	12.5 ± 1.2 ka 20,190–19,330 to 22,560 –21,910	Very coarse, dark brown sand with sub-rounded grains. 7.5 YR 3/2 Dark Brown.
294 295 296	LBCS	Otis	0.56	–	Loosely-compacted coarse-grained grey sands. Largely archaeologically-sterile. 7.5 YR 3/2 Black.
297 298 299	LBCS	Ollie	0.59	22,560–21,910 to 23,080 –22,610 22.1 ± 1.3 ka (OSL)	Stratified combustion feature deposits. 7.5 YR 2/2 Very dark brown.
300 301 302	LBCS	Kate	0.71	–	Loosely-compacted, moist, coarse sands. 2.5 YR 4/4 Reddish brown.
304 305 337	LBCS	Colton	0.81	22,560–21,910 to 23,080 –22,610 27.8 ± 2.1 ka (OSL)	Loosely-compacted, moist coarse sands. 10 YR 5/4 Light olive brown.
				– 37.6 ± 4.2 ka (OSL)	

mass spectrometry model from 11,000 cal yr BP to ca. 10,500 cal yr BP (Fisher et al., 2020). Thus, the deposits at Waterfall Bluff reveal a continuous occupation from MIS 3 to the Early Holocene (Fisher et al., 2020). Archaeological material recovered from the excavations as well as specialist samples for various analysis (e.g., micromorphology, dating samples, charcoal and sediment samples for archaeobotanical analysis) were plotted in 3D using total stations (Fisher et al., 2020). To date, >25,000 artifacts and faunal (terrestrial and marine) remains have been recorded.

2.2. Regional setting

Mpondoland extends approximately 50 km along the East Coast of South Africa from the Mthatha River in the south to the Mtamvuna River in the north (Fig. 1). Our study area lies in the Lambasi District of Eastern Mpondoland (Eastern Cape Province), also known as the Wild Coast, where the coastal landscape is characterised by plateau plains and rolling hills, deeply incised valleys, and deep gorges carved into the Devonian-aged Msikaba Formation sandstones.

The Indian Ocean Coastal Belt (IOCB) is widespread along the coasts of Mpondoland, which in South Africa constitutes an 800 km-long coastal strip from the Mozambique border to the mouth of the Great Kei River in the Eastern Cape Province of South Africa (Fig. 1a). Present-day rainfall in the region falls predominantly during austral summer with mean annual precipitation reaching ~1120 mm/year (Bailey, 1979; Camp, 1999; Cawe, 1994). Closer to the coast, rainfall is less seasonal and frost occurs infrequently (Cawe, 1994). Our study area has one of the highest proportions of winter rainfall among other coastal areas of the IOCB (up to 36.6% rainfall in winter; Cawe, 1994). Current regional vegetation comprises a mosaic of sourveld grassland (Pondoland-

Ugu Sandstone Coastal Sourveld, IOCB; Mucina et al., 2006b), bushveld (Eastern Valley Bushveld, Savanna biome, Rutherford et al., 2006) and forest vegetation (Scarp Forest; Southern Coastal Forest, along the coast; Southern Mistbelt Forest further inland in altitudes between 850 and 1,100 m above sea level; Mucina and Geldenhuys, 2006) (Fig. 1b). Sourveld grassland vegetation is dominated by natural species-rich grasslands of low nutrient grasses (i.e. Panicoideae; Shackleton et al., 1991) with scattered low shrubs or small trees (Fig. 2E and F). This unit is restricted to the Msikaba Formation sandstones on the neocoastal peneplain. Bushveld vegetation –mosaics of semi-deciduous savanna woodlands and thickets often dominated by succulent members of the genera *Euphorbia* and *Aloe*– is common in fire-resistant pockets, in small gullies, and in rocky outcrops. The Coastal and Scarp Forests have a large diversity of woody (trees and shrub) species with many endemics (Van Wyk and Smith, 2001). Low Coastal Forests occur along coastal dunes, and are dominated by a low tree canopy (i.e., *Celtis africana*, *Sideroxylon inerme*, *Mimusops caffra* and *Dovyalis rotundifolia*), shrubs (i.e., *Brachylaena discolor*, *Strychnos decussata*, *Euclea natalensis* and *Dracaena aletiformis*) and a herbaceous dicotyledonous (hereafter, dicot) layer (Mucina and Geldenhuys, 2006) (Fig. 2 A and B). Scarp Forests grow at the coast or in deep gorges, often associated with river cliffs and scarps, and coastal platforms. These are tall, species-rich and structurally diverse, multi-layered forests with a well-developed canopy and understorey tree layers (e.g., *Buxus* species, *Drypetes gerrardii*, *Englerophyllum natalense*, and *Heywoodia lucens*), but with a poor herbaceous layer (Fig. 2B and C). Southern Mistbelt forest is a species-rich afrotemperate forest comprised of subtropical floral elements (i.e., *Afrocarpus falcatus*, *Podocarpus henkelii* and *Celtis africana*).



Fig. 2. Waterfall Bluff rock shelter and important vegetation types. Panoramic view of Waterfall Bluff cascade and rock shelter and Mlambomkulu river, taken with a DJI Mavic Pro. Photographs of recurrent vegetation types present in the study region and discussed along the text are given here as a graphical illustrations. **A, B.** Coastal forests; **C, D.** Scarp forests; **E, F.** Sourveld grasslands. WB, Waterfall Bluff rock shelter.

3. Materials and methods

3.1. Materials

In 2016, 33 sediment samples were collected from the N850E321NW vertical section at Waterfall Bluff's dripline for pollen, phytolith and plant wax isotope analyses (Figs. 3 and 4 and Table 1). This area provided the most detailed stratigraphic sequence showing 11 SubAggs at the time of the collection (Fig. 4), but subsequent research has revealed a more comprehensive stratigraphy further inside the rock shelter (Fisher et al., 2020). We recognize that the N850E321NW section has been heavily influenced by drip water, impacting the preservation of the deposits as well as faunal and botanic remains in this area. Therefore, to enrich this study, we have also included 46 plant fragments and 43 charcoal fragments. Of the 43 charcoal fragments, 24 come from the LBCS deposits that date from MIS 3 to the LGIT (Fig. 3 and Table 2) and 19 come from the SRCS deposits that date to the Early Holocene. All plant fragments are derived from the SRCS deposits dating to the Early Holocene (Table 3). The provenance of the material here studied (sediment samples, charcoal and plant fragments) was recorded in 3D using total stations (see Fig. 3).

3.2. Methods

3.2.1. Charcoal and other macrobotanical remains

Charcoal fragments were viewed using a binocular microscope (Olympus SZX16, magnification $\times 7$ –112), and fractured to reveal fresh surfaces of the three planes required to observe anatomical features (transverse, radial longitudinal and tangential longitudinal). Wood anatomy was studied under higher magnification ($\times 200$ –500; Zeiss Axiolab-A1 bright phase/dark phase reflected light microscope) and photographed with an Olympus DP72 digital camera and Stream Essentials software. Charcoal was identified using the features of the tissues (vessels, parenchyma and rays) and cells (size, pitting and inclusions) and directly compared with modern comparative charcoal collections housed at the University of the Witwatersrand's Archaeology Department and the Evolutionary Studies Institute (ESI). These collections are incomplete for the South African flora, so the computer identification program for modern woods, "Inside Wood" was consulted. Terminology follows that of the IAWA Committee (Wheeler et al., 1989). Macrobotanical remains were all too small or disintegrated for taxonomic identification by the time of analysis, and only higher taxonomic levels have been described.

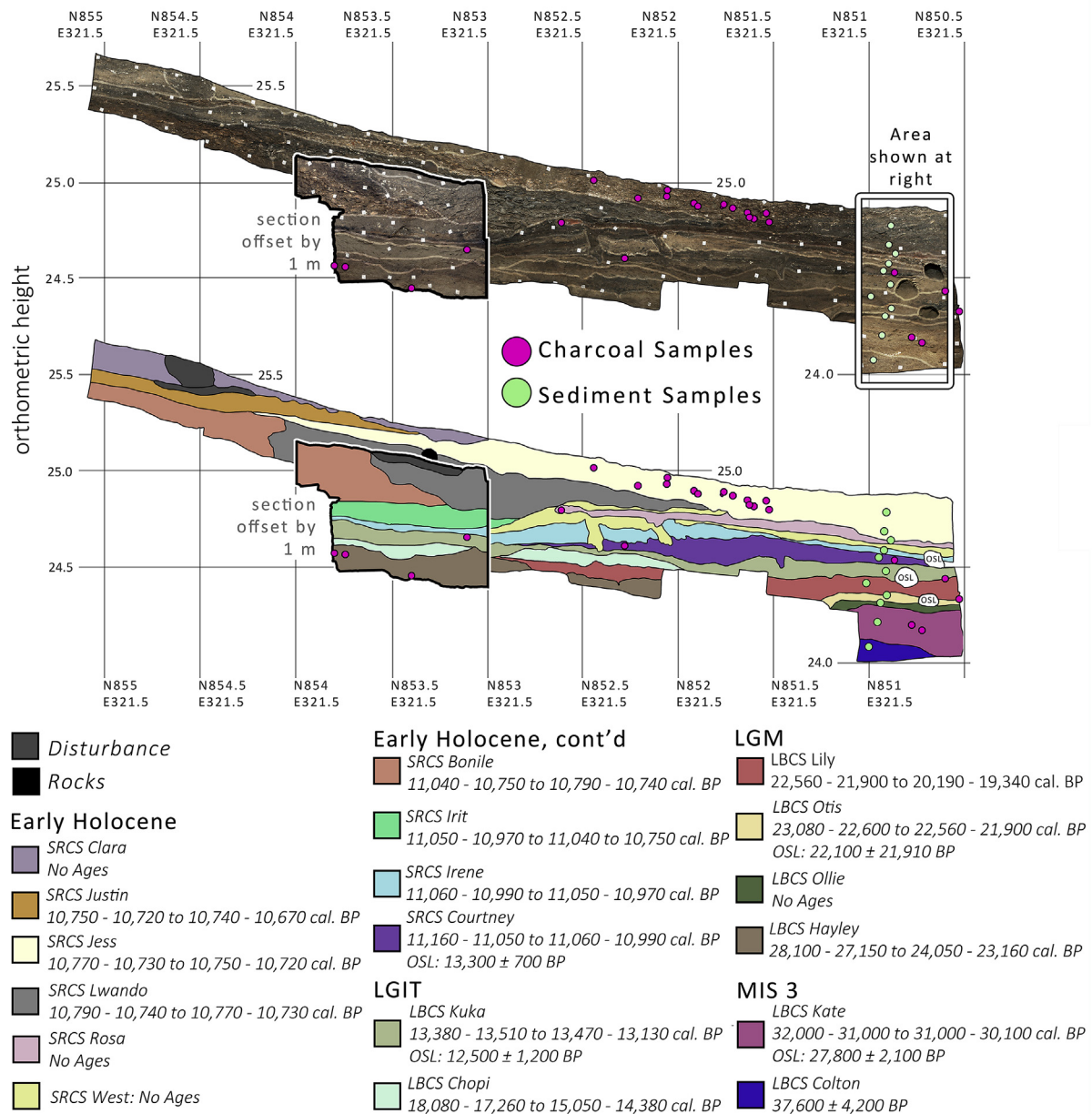


Fig. 3. Stratigraphic silhouette of Waterfall Bluff. The complete stratigraphic silhouette of the E321.5 profile (left), the N850.5 profile (centre) and the E321 profile shows the provenance of the vertical profile here studied for pollen, phytolith and plant wax isotope analyses (green dots) and charcoal samples (pink dots). Indication on SubAggregate boundaries is also given by providing a colour key reference for each SubAggregate, and ages. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2.2. Phytolith analysis

We extracted and analysed sediment samples for their phytoliths at the ESI, following the method developed by Katz et al. (2010). Prior to this, organic matter was oxidised using hydrogen peroxide (H_2O_2 33%). Morphological identification was based on South African modern plant reference collections (Cordova, 2013; Cordova and Scott, 2010; Esteban et al., 2017b; Murungi, 2017; Murungi and Bamford, 2020; Novello et al., 2018; Rossouw, 2009) and the online phytolith database – PhytCore (<http://www.phytcore.org>). Descriptions and naming of the phytoliths follows the International Code for Phytolith Nomenclature 2.0 (ICPN, Neumann et al., 2019). Phytolith morphotype names have been written in small capitals following the recommendations of the ICPN after Joosten and De Klerk (2002). Diatoms and sponge

spicules were also counted but taxonomical identifications were not conducted.

3.2.3. Palynology

We processed and extracted palynomorphs (pollen, spores and other acid-resistant microfossils like fungal remains) from sediment samples at the ESI, following standard procedures after Faegri et al., 1989). The slides were studied under an Olympus CX23 petrographic microscope at 400× and 1000× magnification. The pollen reference collections at the ESI, as well as reference literature (e.g., Bonnefille and Rioulet, 1980; Scott, 1982b), were used for identification.

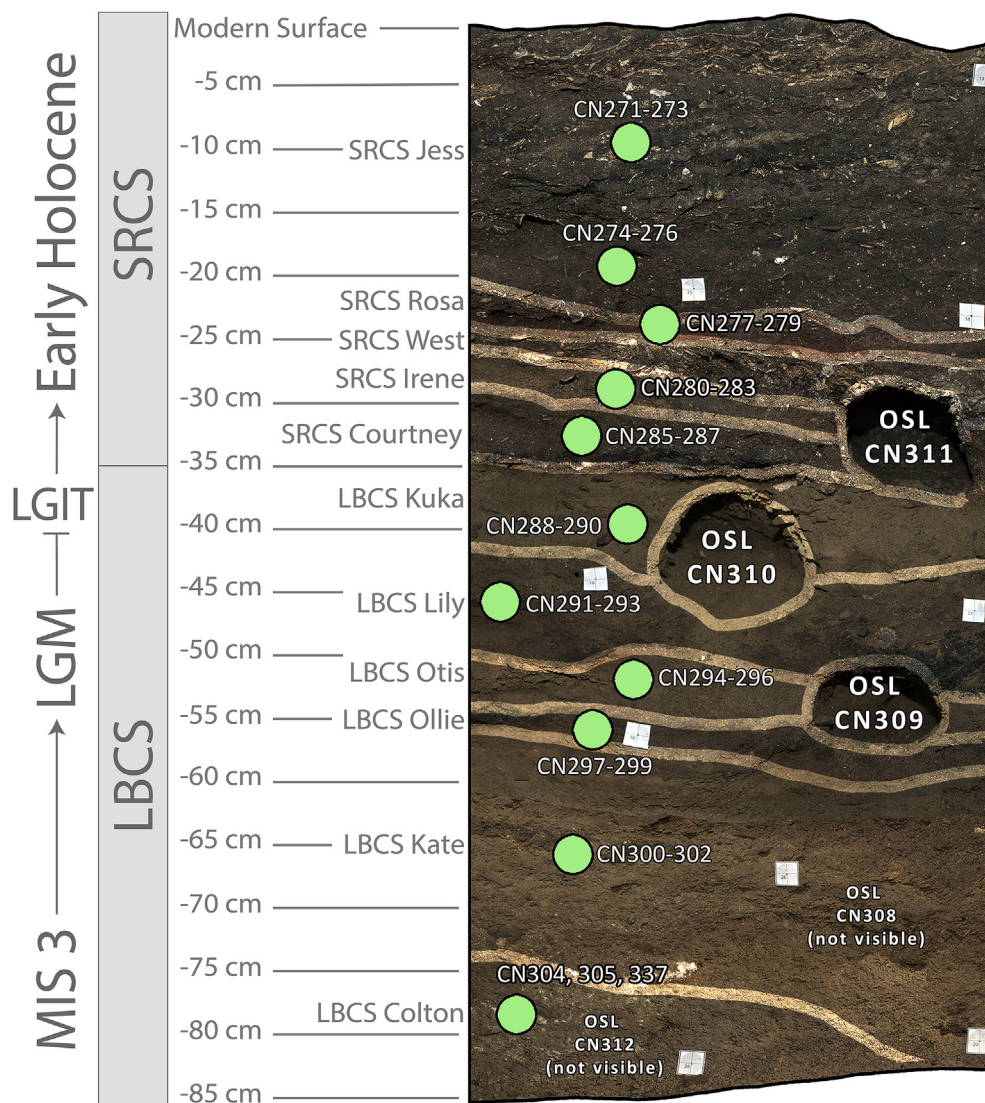


Fig. 4. N850E321NW Vertical Section of Waterfall Bluff. This figure provides detail provenance of the vertical profile here studied for pollen, phytolith and plant wax isotope analyses and sample location (green dots) by giving stratigraphic provenance, depth below the surface (in meters) and chronostratigraphic information. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2.4. Plant wax analyses

Dried and ground sediments were extracted using a dichloromethane (DCM): methanol (MeOH) (9:1, v/v) mixture. Squalane was added prior to extraction as internal standard. After saponification and extraction of the neutral fractions with hexane, silica column chromatography was used to split the neutral fractions into hydrocarbon, ketone and polar fractions, eluting with hexane, DCM and DCM:MeOH (1:1), respectively. The hydrocarbon fractions were eluted with hexane over AgNO₃-impregnated silica columns to obtain saturated hydrocarbon fractions.

The concentrations of long-chain *n*-alkanes were measured using a Thermo Fischer Scientific Focus gas-chromatograph (GC) with flame-ionization-detection (FID). Concentrations were estimated by comparison with an external standard containing known amounts of *n*-alkanes (C₁₉–C₃₄) run every 5 samples. Replicate analyses of the external standard yielded a quantification uncertainty of <5%.

The stable carbon isotope composition ($\delta^{13}\text{C}$ in ‰ VPDB) of long chain *n*-alkanes ($^{13}\text{C}_{\text{wax}}$) was measured using a Thermo Trace GC coupled to a Finnigan MAT 252 isotope ratio monitoring mass

spectrometer. The $\delta^{13}\text{C}$ values were calibrated against external CO₂ reference gas. Samples were run at least in duplicate. The internal standard yielded an accuracy of 0.1‰ and a precision of 0.1‰ ($n = 11$). An external standard was analysed every 6 runs. The long-term precision and accuracy of the external *n*-alkane standard containing 16 externally calibrated *n*-alkanes was 0.2 and 0.1‰.

The stable hydrogen isotopic composition (δD in ‰ versus VSMOW) of long chain *n*-alkanes ($\delta\text{D}_{\text{wax}}$) was measured using a Thermo Trace GC coupled to a Thermo Fisher MAT 253 isotope ratio mass spectrometer. The δD values were calibrated against external H₂ reference gas. The H₂³ factor fluctuated around 5.2 ppm nA⁻¹ during analyses and was monitored daily. Samples were run at least in duplicate. The internal standard yielded an accuracy of 3‰ and a precision of 1‰ ($n = 11$). The long-term precision and accuracy of the external standard mixture run every sixth analysis was 3 and < 1‰, respectively. The δD values of the plant waxes are corrected to account for the effect of ice volume changes on isotopes in the global hydrological cycle (i.e., Collins et al., 2013; Niedermeyer et al., 2016; Schefuß et al., 2005) using the benthic foraminifera isotope data from Bintanja et al. (2005).

Table 2

List of charcoal samples taxonomically identified. EC = Eastern Cape Province, KZN = KwaZulu Natal Province, LIM = Limpopo Province, M = Mpumalanga Province, WC = Western Cape Province, MZ = Mozambique, SZ = Eswatini, ZW = Zimbabwe, SRZ = summer rainfall zone of southern Africa. Distribution of tree taxa can be consulted in [van Wyk and van Wyk, 2013](#)), [Coates-Palgrave \(2002\)](#) [Germishuizen and Meyer \(2003\)](#). See [Fig. 3](#) for stratigraphic location and information.

StratAgg	SubAgg	Family	Genus and Species	Growth form	Resource significance, habitat and distribution	References of medicinal uses
SRCS	Jess	Simaroubaceae	<i>Kirkia wilmsii</i> Engl.	Small to medium tree	Bark yields a strong fibre; dry bushveld and rocky places; LIM, M.	
SRCS	Jess	Tiliaceae	<i>Grewia flavescens</i> Juss.	Multi-stemmed shrub	Bushveld; LIM, M, KZN.	
SRCS	Jess	Sapindaceae	<i>Hippobromus pauciflorus</i> L.f. Radlk	Shrub or small tree	Leaves, bark and root used medicinally although leaves and roots are poisonous; forest margins; M, KZN, EC coast.	Pendota et al. (2009)
SRCS	Jess	Icacinaeae	cf. <i>Apodytes dimidiata</i> E. Mey. Ex Arn.	Small to large evergreen tree	Wood very hard; root and leaves used medicinally; coastal and inland forest; LIM, M, KZN, EC, WC.	Foubert et al. (2011) ; Masoko and Nxumalo, (2013) ; Mmushi et al. (2010)
SRCS	Jess	Arecaceae	—	—	—	
SRCS	Jess	Fabaceae	<i>Millettia</i> sp. [possibly <i>grandis</i>]	Small to medium tree	—	Obiri et al. (2002) ; van Wyk and Gericke, (2000)
SRCS	Jess	Fabaceae	—	—	—	
SRCS	Jess	Fabaceae	<i>Millettia grandis</i> E. Mey. Skeels	Small to medium tree	Wood hard and durable; roots and seeds used medicinally and as poison; coastal forests and forest margins; KZN, EC coast.	Obiri et al. (2002) ; van Wyk and Gericke, (2000)
SRCS	Jess	Fabaceae	<i>Schotia brachypetala</i> Sond.	Medium to tall tree	Hard wood, edible seeds, traditional medicine; Coastal and riverine forest, bushveld; EC, KZN, MP, LIM into MZ and ZW	
SRCS	Lwando	Sterculioideae	<i>Dombeya tiliacea</i> Endl. Planch	Shrub or small tree	Very hard wood; forest margins and valley bushveld; KZN, EC coast.	
SRCS	Irit	Fabaceae	<i>Millettia grandis</i> E. Mey. Skeels	Small to medium tree	Hard wood used for e.g. digging sticks, ground seed used as arrow poison (hunting; forest and forest margins, drought resistant; KZN, EC, common in Mpondoland.	Obiri et al. (2002) ; van Wyk and Gericke, (2000)
SRCS	Irit	Icacinaeae	<i>Apodytes dimidiata</i> E. Mey. ex Arn. subsp. <i>dimidiata</i>	Small bushy tree	Hard wood, important traditional medicine tree; coastal forest, open bushveld, grassland and rocky areas; WC, EC, KZN, G.	Foubert et al. (2011) ; Masoko and Nxumalo, (2013) ; Mmushi et al. (2010)
LBCS	Kuka	Olaceae	<i>Ximenia caffra</i> Sond.	Branched shrub or small tree	Bark and leaves used medicinally; edible fruit; bushveld and coastal bush; LIM, M, KZN.	De Wet et al. (2012) ; Fabry et al. (1998) ; Mulaudzi et al. (2011) ; Munodawafa et al. (2013) ; Nair et al. (2013) ; Zhen et al. (2015)
LBCS	Chopi	Icacinaeae	<i>Apodytes dimidiata</i> E. Mey. ex Arn. subsp. <i>dimidiata</i>	Small bushy tree	Hard wood, important traditional medicine tree; coastal forest, open bushveld, grassland and rocky areas; WC, EC, KZN, G.	Foubert et al. (2011) ; Masoko and Nxumalo, (2013) ; Mmushi et al. (2010)
LBCS	Chopi	Apocynaceae	<i>Rauvolfia caffra</i> Sond.	Small to large tree	Medicinal; indicator of groundwater; watercourses, coastal forest and forest margins; EC, KZN, MP, LIM, G, NW.	Milugo et al. (2013) ; Steenkamp et al. (2007)
LBCS	Chopi	Anacardiaceae	<i>Lannea discolor</i> Sond. Engl.	Deciduous, medium tree	Edible fruit; traditional medicine; bushveld and rocky ridges; KZN, MP, G, NW.	Coates-Palgrave, (2005) ; van Wyk and Gericke, (2000)
LBCS	Chopi	Malvaceae	<i>Dombeya rotundifolia</i> Hochst.	Small tree	Medicinal plant; many traditional uses; woodland, grassland and rocky mountain slopes; KZN, MP.	McGaw et al. (2000)
LBCS	Chopi	Rhamnaceae	<i>Ziziphus mucronata</i> Willd.	Small to medium tree	Edible fruits and many magico-medicinal uses; wide range of habitats; SRZ	Chauke et al. (2015) ; McGaw et al. (2000)
LBCS	Chopi	Oleaceae	<i>Olea capensis</i> L.	Shrub or small to medium tree	Very heavy, hard wood difficult to collect, used for firewood; forest margins, rocky bushveld; WC, EC, KZN, MP, LIM.	
LBCS	Chopi	Fabaceae	<i>Millettia grandis</i> E. Mey. Skeels	Small to medium tree	Hard wood used for e.g. digging sticks; ground seed used as arrow poison (hunting; forest and forest margins, drought resistant; KZN, EC, most common in Mpondoland.	Obiri et al. (2002) ; van Wyk and Gericke, (2000)
LBCS	Hayley	Boraginaceae	<i>Cordia caffra</i> Sond.	Shrub or small to medium tree	Medicinal treatment for eyes. Fire sticks to make fire by friction; coastal and riverine forest; Transkei coastal belt up to MZ.	Poolely, (1993) ; van Wyk and Gericke, (2000)
LBCS	Kate	Oleaceae	<i>Olea</i> sp.	Medium to large tree	Hard, heavy wood, edible fruit; deciduous forests; EC, KZN, LIM, M.	
LBCS	Kate	Oleaceae	<i>Olea</i> sp.	Medium to large tree	Hard, heavy wood, edible fruit; deciduous forests; EC, KZN, LIM, M.	
LBCS	Kate	Rubiaceae	<i>Canthium inerme</i> L.f. Kuntze	Shrub or small to medium tree	Heavy, hard wood, edible fruit, also used in traditional medicine; variety of habitats including forest bushveld and rocky grasslands; WC, EC, KZN, MP, LIM, SZ, MZ and ZW.	McGaw et al. (2000)
LBCS	Kate	Moraceae	<i>Ficus</i> sp. [possibly <i>bizanae</i>]	Medium to tall tree	Medicinal; coastal forest; EC, KZN, endemic to Mpondoland.	Chauke et al. (2015) ; Maroyi (2013)
LBCS	Kate	Rhizophoraceae	<i>Cassipourea</i> sp. [possibly <i>flanagani</i>]	Small to medium tree	Bark harvested for traditional medicine, cosmetics; coastal forest; EC, KZN.	Cocks and Dold (2004, 2014)
LBCS	Kate	Rosaceae?	—	—	—	

Table 3
List and numbers of plant fragments from the various stratigraphic entities. None were identifiable to taxon level.

Plant fragment	Stratigraphic entities (SRCS SubAggs)					
	Total	Jess	Justin	Lwando	Bonile	Rosa
Dicotyledonous leaves	11	0	9	0	2	0
Grass (Poaceae) leaves	6	1	5	0	0	0
Indeterminate	15	2	2	3	7	1
Monocotyledonous leaves	2	0	1	1	0	0
Pod fragment	1	1		0	0	0
Stems (probably from dicots)	6	5	1	0	0	0
Seeds (indeterminate)	5		4	1	0	0
TOTAL	46	9	22	5	9	1

To assess the level of degradation of the plant waxes, we calculated the carbon preference index (CPI; Bray and Evans, 1961). The CPI reflects the molecular distribution of odd-to-even *n*-alkanes within a specific carbon number range (here *n*-C₂₄ to *n*-C₃₄). High CPI values (>5) indicate a significant contribution of waxes from terrestrial plants and low levels of degradation while low CPI values indicate low input of plant waxes from terrestrial plants or high degradation (Eglinton and Hamilton, 1967).

$CPI_{25-33} = 0.5 * (\Sigma C_{odd27-33} / \Sigma C_{even26-32} + \Sigma C_{odd27-33} / \Sigma C_{even28-34})$ with *C_x* the amount of each homologue.

4. Results

4.1. Macrobotanical remains

A total of 27 out of 43 charcoal fragments were taxonomically identified, with 24 samples being identified to genus/species level

and three tentatively to family level (Table 2). From the current sample set, 15 charcoal fragments are from LBCS deposits and 12 from the SRCS (Table 2).

MIS 3: to date, 12 charcoal fragments have been studied from deposits dating to MIS 3, and 5 were identified to genus and species level (Table 2). The identified species include typical coastal forest taxa such as *Ficus* sp. [possibly *bizanae*] and *Cassipourea* sp. [possibly *flanagani*].

LGM: out of the two charcoal fragments studied from these deposits, only one was identified to species level, *Cordia caffra*, which currently occurs along the coastal belt of the Wild Coast (Table 2).

LGIT: eight of the 10 charcoal fragments studied from these deposits were identified to species level. The identified taxa include typical bushveld (*Ximenia caffra*, *Apodytes dimidiata* subsp. *dimidiata*, *Lannea discolor*, *Dombeya rotundifolia* and *Olea capensis*) and coastal (*Rauvolfia caffra* and *Milletia grandis*) species (Table 2).

Early Holocene: ten of the 19 charcoal fragments studied from these deposits were identified to species level, and two to family level. The identified species include *Apodytes dimidiata*, *Dombeya tiliacea*, *Hippobromus pauciflora*, *Milletia grandis*, *Kirkia wilmsii* and *Grewia flavescens* (Table 2). Many whole and fragmentary leaves were also found preserved and particularly from SRCS Justin, Lwando, and Bonile (Fig. 3). Most macrobotanical remains were found adhering to the underside of mussel shells (i.e., *Perna perna*; see Fisher et al., 2020 for further information), which shielded these fragile plant remains. Unfortunately, the plant remains dried quickly after excavation and rapidly disintegrated; they were too small to determine the shape, size and venation of the leaf, except to distinguish between dicot and monocot (grasses and sedges) leaves. The twigs belonged to dicots and have no distinguishing

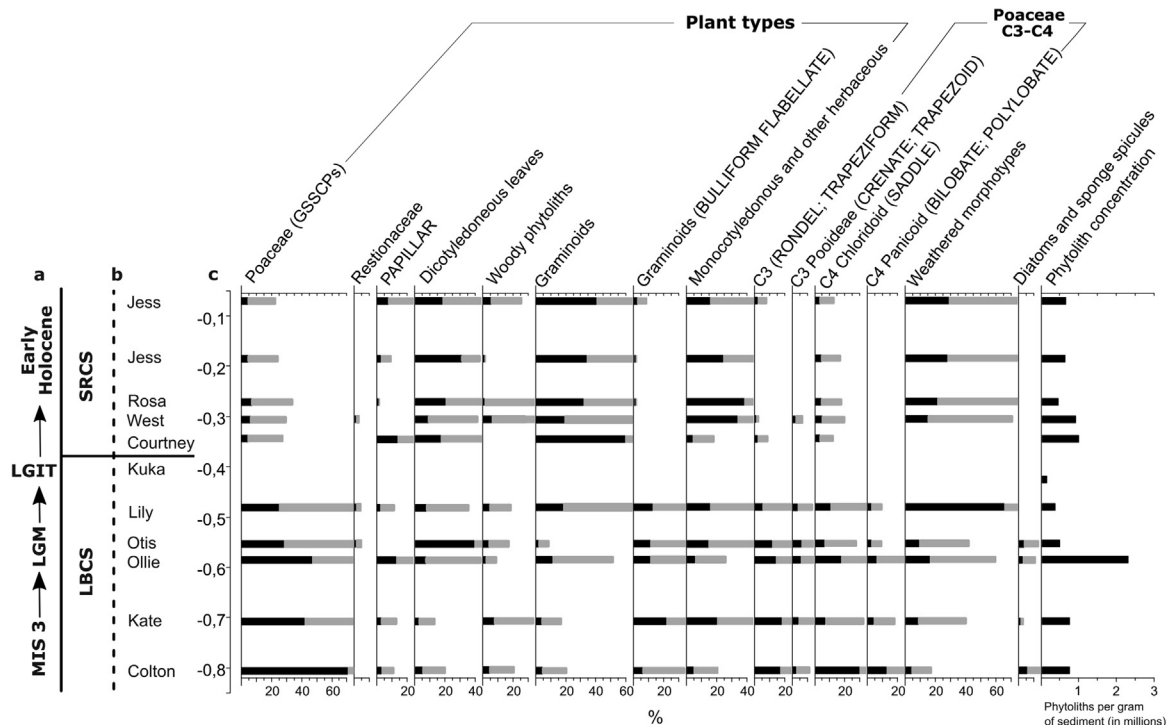


Fig. 5. Phytolith histogram of the vertical transect at Waterfall Bluff. Phytolith information is provided giving stratigraphic provenance, depth below the surface (in meters), and the frequencies of the most significant plant contributions, weathered morphotypes, bio-silica algal remains (diatoms and sponge spicules) and phytolith concentration (millions of phytoliths per gram of sediment). Grey bars are the x5 exaggeration. MIS 3-Marine Isotope Stage 3, LGM-Last Glacial Maximum, LGIT-last glacial/interglacial transition. a) Chrono-geologic/climatic period; b) Stratigraphic provenance; c) Depth below the surface (meters). Graminoids include Elongate columnar, crenate, dentate, echinate, ligulate and sinuate. Monocotyledonous and other herbaceous include Elongate entire, facetate/velloate and granulate. The phytolith percentage histogram was constructed with TILIA 1.7.16, using morphotaxa as the phytolith sum.

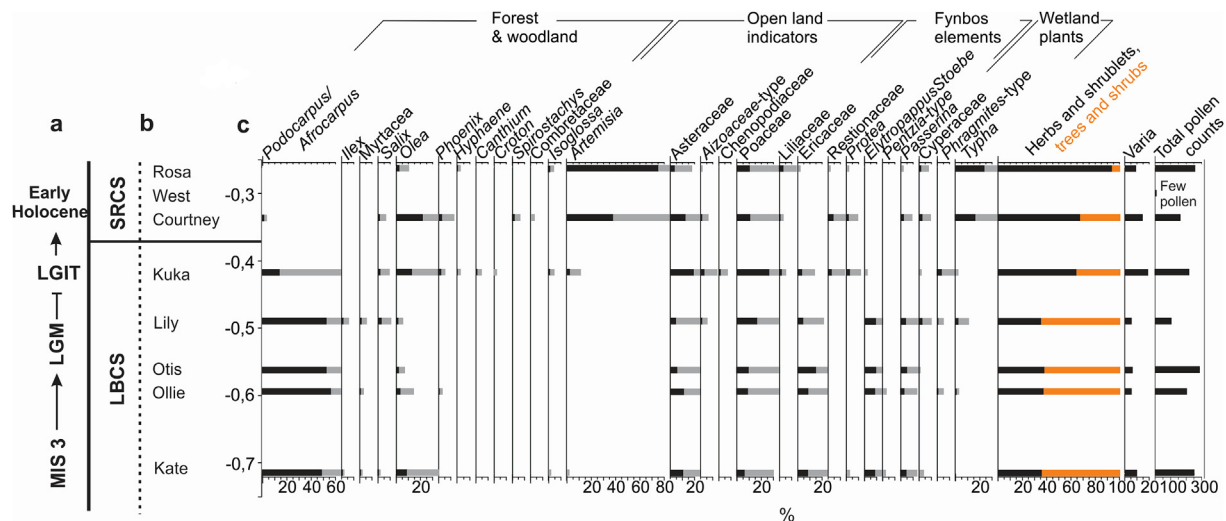


Fig. 6. Pollen histogram of the vertical transect at Waterfall Bluff. Pollen data is provided giving stratigraphic provenance, depth below the surface (in meters), ecological groups (forest and woodland, open land indicators, fynbos elements, wetland plants), and the ecologically most important taxa are shown. Grey bars are the x5 exaggeration. MIS 3–Marine Isotope Stage 3, LGM–last glacial maximum, LGIT–last glacial/interglacial transition. a, Chrono-geologic/climatic period; b, Stratigraphic provenance; c, Depth below the surface (meters). The palynological percentage histogram was constructed with TILIA 1.7.16, using the terrestrial taxa as the pollen sum.

features. Steps have been taken since to ensure the preservation of future excavated macrobotanical remains. Table 3 lists identifications from each plant fragment studied and their SubAggs.

4.2. Phytoliths

Phytoliths were identified in all 11 samples varying from 0.12 to 2.3 million phytoliths per gram of sediment (hereafter referred to only as millions of phytoliths; Fig. 5). Phytolith concentrations increased from the base to the top of the vertical transect, except for the sample from LBCS Ollie, which had the highest phytolith concentration of all the analysed samples (2.3 million phytoliths). The oldest deposits, LBCS Colton and Kate, dating to MIS 3, contained the highest percentage of bio-silica algal remains (diatoms and sponge spicules). These were absent in deposits dating to the LGM, LGIT and Early Holocene. Weathered morphotypes (chemically altered phytoliths) were identified in all analysed samples (Fig. 5). A total of 63 phytolith morphotypes were identified, which were later clustered in 26 general morphotype groups (see Phytolith Data in Supplementary Table 1). These were further grouped into 12 general categories (Fig. 5). The uppermost LBCS SubAgg Kuka dating to the LGIT was not considered for interpretation due to poor phytolith preservation.

MIS 3: These deposits contained the highest frequencies of grass phytoliths (Fig. 5). C₄ Panicoideae (hereafter panicoids) grass silica short cell phytoliths (GSSCP) Bilobate dominates in LBCS Colton, although C₄ Chloridoideae GSSCP Saddles (hereafter – chloridoids) are also well represented (48% and 20% of the total sum, respectively; Fig. 5). In overlying LBCS layer Kate, the grass phytolith component decreases notably and comprises mostly Rondels and other trapeziforms (68.5% of the total sum). The phytolith assemblage from the undated LBCS Ollie comprises a high graminoid component, with GSSCPs (Poaceae) making up to 42%, and Papillar phytoliths (these are the leaf/culm cones of Murungi and Bamford, 2020), which belong to the Cyperaceae family, peaking at 12.1% (Fig. 5).

LGM: Grass phytolith concentrations decrease from MIS 3 to the LGM. LBCS Otis, for instance, is characterized by a low presence of GSSCPs, and mostly of trapeziform forms (Fig. 5). It is important to note the increase in GSSCPs Crenate and trapezoid, which are

associated to the Pooideae subfamily (23%; Rossouw, 2009). Conversely, dicot leaf phytoliths are recorded here in the highest frequency (40%) across the Waterfall Bluff sequence. Restionaceae and Papillar phytoliths were also observed, but in lower frequencies (0.9 and 1.9%, respectively; Fig. 5).

Early Holocene: Grass phytoliths are scarce in the SRCS deposits, and dicot leaf phytoliths, from either trees and/or shrubs, and Elongates with decorated margins increase (Fig. 5). Restionaceae phytoliths are also identified in sediments from SRCS West. Finally, Papillar phytoliths are identified in most of the samples, peaking at 12.9% during SRCS Courtney and 7% during Waterfall Bluff's last occupation in SRCS Jess.

4.3. Palynology

The terrestrial pollen sum for the 7 samples, which were included in the pollen histogram, vary between 95 and 288 (Fig. 6). Due to the discontinuous nature of the palynological record, we depicted the percentages of the palynomorphs in a histogram rather than in curves. Three samples from SRCS (CN271, SRCS Jess; CN274, SRCS Jess Lower; CN280, SRCS West) and 1 from LBCS Colton (CN304) had to be disregarded due to their low pollen sum (1–20 pollen grains/sample). Percentages of varia pollen (crumpled, corroded and, therefore, indeterminate pollen grains) are also high (5.3–18.8%; Fig. 6) which hampered the interpretation of the pollen record. A pollen-zonation on the basis of pollen and spore composition and relative abundance of certain species was not done due to the low number of samples and the discontinuous character of the sequence. Instead, the Waterfall Bluff pollen sequence was subdivided into chrono-stratigraphic zones (MIS 3, LGM, LGIT, Early Holocene; Fig. 6).

MIS 3: LBCS Kate is characterised by a high contribution of *Podocarpus/Afrocarpus* pollen (49%). Pollen of *Olea* was the second most prolific woodland elements at Waterfall Bluff (9%). Asteraceae pollen, a family with many species occurring in open grasslands, are represented at 11%. Fynbos/renosterveld taxa (*Ericaceae* and *Stoebe/Elytropappus* pollen; Scott, 1987) occur at 8–9%, whereas pollen of both *Protea* and *Restionaceae* are rare at Waterfall Bluff. *Passerina*, often a part of coastal vegetation (i.e., dune fynbos; Mucina et al., 2006a), also occur regularly (~5%). Poaceae is

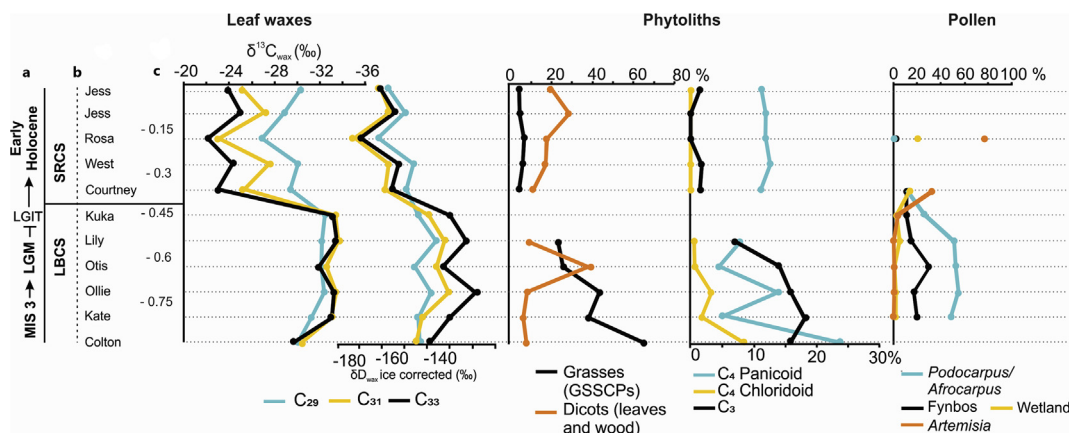


Fig. 7. Hydroclimate and photosynthetic vegetation type reconstruction at Waterfall Bluff based on plant waxes. a) Hydrogen isotope composition of C_{29} , C_{31} and C_{33} n -alkanes, reflecting changes in moisture availability. b) Stable carbon isotope composition of C_{29} , C_{31} and C_{33} n -alkanes, mainly reflecting changes in C_3/C_4 vegetation type. MIS 3-Marine Isotope Stage 3, LGM-last glacial maximum, LGIT-last glacial/interglacial transition. a, Chrono-geologic/climatic period; b, Stratigraphic provenance; c, Depth below the surface (meters).

represented only at 6%, while wetland elements were negligible (<1%). Located in between LBCS Kate (MIS 3) and LBCS Otis (LGM), the LBCS Ollie pollen record is similar to LBCS Kate, with a slight increase in podocarp pollen up to 56% and a decrease in *Olea* to 1%.

LGM: During the LGM at Waterfall Bluff (LBSC Otis and Lily) tree pollen (i.e., *Podocarpus*/*Afrocarpus* and *Olea*) percentages increased to 62–64%. In LBSC Otis, pollen of the fynbos/renosterveld taxa Ericaceae and *Elytropappus/Stoebe* (represented at 14% and 8–9%, respectively) occurred alongside the high *Podocarpus*/*Afrocarpus* pollen percentages. LBSC Lily might mark a slight change in the vegetation composition at Waterfall Bluff with an increase in Poaceae pollen from ~10% to ~16%, whereas Asteraceae slightly declined from ~10% to 4%. Wetland/riverine-indicative pollen such as *Salix*, Myrtaceae, Cyperaceae and *Typha* were well represented in LBSC Lily (Fig. 6).

LGIT: An abrupt change in the Waterfall Bluff pollen record occurs in LBCS Kuka. Tree pollen percentages drop to ~34%. *Podocarpus/Afrocarpus* pollen decreases from 53% in LBCS Lily to 14% in LBCS Kuka. *Isoglossa* pollen, a herb known to grow in forest understoreys (Poolley, 1998), appears at this time. Furthermore, *Olea* pollen reaches a maximum of 12%. Pollen of palms, *Phoenix* and *Hyphaene*, is present but in low percentages. Conversely, fynbos/renosterveld pollen taxa especially *Elytropappus/Stoebe* decreases, and pollen of Poaceae and Asteraceae, including *Artemisia*, increase. Aizoaceae and Amaranthaceae pollen are also detected more often (Fig. 6). For the first time, Liliaceae pollen grains are identified. Pollen of *Phragmites* is present whereas all other wetland elements are low. LBCS Kuka shows the highest percentage of varia pollen (19%) throughout the pollen profile.

Early Holocene: Out of the five samples analysed from SRCS only two contain pollen in sufficient numbers (SRCS Courtney and Rosa), which are also characterised by a high percentage of varial pollen (~9–14%). In SRCS Courtney, *Podocarpus*/*Afrocarpus* pollen decreases to <1%, while *Olea* pollen increases (~22%). Pollen of warmth demanding woodland taxa like *Combretaceae* and *Spirostachys* also occur for the first time. Pollen of wetland elements (*Typha* and *Cyperaceae*) are much more prominent in these deposits. *Phoenix* pollen reaches the highest percentage (2.5%) for the sequence. Asteraceae percentages were moderate but a sharp increase in *Artemisia* is noted and mainly in SRCS Rosa (~90%). *Artemisia* pollen clumps are common.

4.4. Plant waxes

The Waterfall Bluff samples contained plant-wax derived *n*-alkanes with carbon chain lengths ranging from C₂₅–C₃₅. Their high concentrations and elevated CPI values (5–11, with an average of 7) in all samples document a consistently high and non-degraded plant-wax input. The *n*-C₃₁ alkane was consistently the most abundant compound in all samples with the *n*-C₃₃ alkane being the second most abundant homologue. Their distributions indicate no wax input from aquatic macrophytes. Stable carbon and hydrogen isotope compositions could reliably be detected for the three most abundant *n*-alkane homologues, i.e., the *n*-C₂₉, the *n*-C₃₁ and the *n*-C₃₃ alkane in all samples. Their $\delta^{13}\text{C}$ values range from –33.6‰ to –22.1‰ VPDB and their δD values (corrected for ice volume changes) range from –123‰ to –172‰ (Fig. 7). Plant-wax Data available in [Supplementary Table 2](#).

MIS 3: The sample analysed from LBCS Colton contained the lowest amount of plant-wax *n*-alkanes. The $\delta^{13}\text{C}$ values of these *n*-alkanes were slightly enriched ($\sim 30\%$) and its δD values were slightly depleted ($\sim 145\%$) compared to the overlying LBCS Kate and Ollie (Fig. 7). LBCS Kate, and the undated LBCS Ollie, showed depleted $\delta^{13}\text{C}$ values ($\sim 33\%$) and relatively enriched δD values ($\sim 140\%$) compared to LBCS Colton (Fig. 7).

LGM: The two samples covering the LGM (LBSC Otis and Lily) did not show substantially different $\delta^{13}\text{C}$ and δD values and distributions compared to the MIS 3 samples.

LGIT: LBCS Kuka showed similar $\delta^{13}\text{C}$ and δD values and distributions compared to the MIS 3 and LGM samples.

Early Holocene: The five samples from the SRCS (Courtney, West, Rosa and Jess) showed substantially enriched $\delta^{13}\text{C}$ values ($\sim 26\%$) and strongly depleted δD values ($\sim 160\%$) compared to the MIS 3 and LGM samples. Observed $\delta^{13}\text{C}$ enrichment with increasing chain length is a typical feature of C_4 plant input (e.g., [Vogts et al., 2009](#)).

5. Discussion

5.1. Taphonomy of proxy signals

The variety of archaeobotanical and biochemical proxies preserved at Waterfall Bluff rock shelter and used in this study presents a unique, albeit challenging, opportunity to investigate the coupled response of coastal movements and climate change to

palaeoenvironments and plant availability, and hunter-gatherer's use of plants in coastal Eastern Mpondoland during Marine Isotope Stage (MIS) 3 (ca. 39–29 ka); the Last Glacial Maximum (LGM; ca. 26.5–19 ka); the last glacial/interglacial transition (LGIT; ca. 17 ka – 11.7 ka) and the Early Holocene (11.7 – ca. 8 ka). We propose that the hunter-gatherer daily foraging radii (~10–15 km; e.g., Kelly, 1995) will be the critical factor for classifying “local” environmental conditions versus natural processes that may bring plant remains to the site from the wider landscape. For most proxies, two pathways are possible – natural vs. anthropogenic input. We surmise that the presence of wood-charcoal in anthropogenic combustion features and macrobotanical remains preserved under shell remains indicates that these remains were most likely introduced directly by humans, thus being representative of the past use of plants by site inhabitants. Yet, we recognize that other plant remains like twigs and charcoal not found in combustion features could be derived from vegetation surrounding the site. Likewise, pollen, phytoliths, and plant waxes that are recovered from archaeological sediments can be derived either from plants introduced into sites by humans or through natural processes like wind, water runoff, and natural vegetation that grows at the site. The presence of phytoliths is likely to provide the most local signal because these remains are normally introduced indirectly as a product of human plant selection (e.g., Cabanes, 2020) or directly via plants growing around the site. Yet, even though grasses were introduced by humans, a C₃ vs C₄ grass human-selection bias is not likely (Esteban et al., 2020b). Aeolian phytolith transport could have also occurred, as phytoliths have been detected to travel long distances as part of aeolian dust (Folger, 1970), favoured in loess deposits (Osterrieth et al., 2009), lowland regions and dry environments with sparse vegetation (Latorre et al., 2012; Madella and Lancelotti, 2012), as well as being carried into lakes by wind (e.g., Aleman et al., 2014) and runoff water. However, there is a lack of studies monitoring phytolith deposition in archaeological cave deposits by wind or other non-human agents. Pollen grains have the potential for travelling the longest distances (>15 km), and thus the greatest potential to reflect mixed local and regional environments. However, pollen and spores can also become part of the archaeological record by human activities that introduce plant material to the site (Bryant and Holloway, 1996).

The high concentrations and un-degraded nature of the plant waxes in Waterfall Bluff deposits suggest that this signal is derived from the close vicinity of the site or from material actively brought into it. Plants from further afield would contribute lesser waxes if not actively selected and transported into the site. Plant wax carbon isotopic compositions ($\delta^{13}\text{C}_{\text{wax}}$) are controlled predominantly by the carbon fixation pathway used by the plants (C₃/C₄/CAM; e.g., Diefendorf and Freimuth, 2017) and will thus mainly reflect the vegetation type surrounding the site. The hydrogen isotope composition of plant-waxes ($\delta\text{D}_{\text{wax}}$) primarily reflects changes in the isotopic composition of the water used during lipid biosynthesis (Sachse et al., 2012). $\delta\text{D}_{\text{wax}}$ is controlled by three main factors: 1) the isotopic composition of precipitation ($\delta\text{D}_{\text{precip}}$); 2) isotopic enrichment in soil and leaf water by evapotranspiration; and 3) vegetation type, as a result of differences in plant-type isotopic fractionation between source water and specific lipids. In the tropics, the $\delta\text{D}_{\text{precip}}$ is predominantly controlled by the ‘amount effect’ with a negative correlation between $\delta\text{D}_{\text{precip}}$ and monthly precipitation amount (Dansgaard, 1964). As the ‘amount effect’ is caused by limited re-evaporation during high intensity rainfall events (Risi et al., 2008), it should rather be termed ‘intensity effect’. Temperature affects $\delta\text{D}_{\text{precip}}$ lead to decreased $\delta\text{D}_{\text{precip}}$ with decreasing condensation temperature (Dansgaard, 1964). The ‘continental effect’ and ‘altitude effect’ have an influence on $\delta\text{D}_{\text{precip}}$ by isotopic rainout when moisture is transported inland or towards

higher altitudes. Furthermore, global ice volume changes affect the isotopes in the global hydrological cycle. During the LGM when global ice volume was high, the lighter isotope was preferentially stored within ice sheets, leaving the residual global ocean water isotopically enriched. In parallel with the interpretation of $\delta^{13}\text{C}_{\text{wax}}$ as reflecting mainly the local vegetation, $\delta\text{D}_{\text{wax}}$ signatures should reflect the local hydro-climatic conditions around the site with depleted $\delta\text{D}_{\text{wax}}$ indicating wetter conditions and vice versa. As $\delta\text{D}_{\text{precip}}$ reflects hydro-climatic conditions in a broader area (due to its control by atmospheric processes) the local $\delta\text{D}_{\text{wax}}$ are indicative of regional (instead of merely local) hydro-climatic conditions.

5.2. Hunter-gatherer plant foraging at Waterfall Bluff

The diversity of the woody species identified in the charcoal suggests specific wood selection behaviours. Since most wood can potentially be used as fuel, the woody taxa represented in the Waterfall Bluff charcoal record are primarily associated with their use as fuel to make fire (Table 2). Many of the identified species have hard wood (e.g., *Apodytes dimidiata*, *Dombeya tiliacea*, *Olea capensis* or *Canthium inerme*; Table 2) that is desirable for longer combustion at higher and more stable temperatures. It is noteworthy, however, that most of the identified taxa are also known for their medicinal uses among indigenous South Africans (e.g., *Apodytes dimidiata*, *Cassipourea flanaganii*; Table 2 and references therein). Typically, their antibacterial, antifungal, anti-inflammatory and antimicrobial properties are reported to treat wounds, infections (e.g., eye), fever, tuberculosis, diarrhoea and even infertility (Table 2 and references therein). Leaves of trees and/or shrubs were actively brought into the site by the inhabitants as indicated by the recovery of unidentified leaf fragments and the high presence of dicot leaf phytoliths, which are usually rare in natural and fossil records (e.g., Esteban et al., 2018; 2017a). The leaves of many of the species are believed to hold medicinal value and it is possible that the preserved leaf fragments and dicot leaf phytoliths identified in these deposits belong to the same species identified in the charcoal assemblage. This suggests that woody plants, both wood and leaves, were brought into the shelter for various purposes, including medicinal treatments.

One particularly good example of a medicinal plant signal may be represented in SRCS Rosa, where an exceptionally high presence of *Artemisia* pollen (>70%) was found. *Artemisia* pollen is transported by wind, so it is often overrepresented in pollen records (Xu et al., 2009) and we recognize that it could have been blown into the site. *Artemisia afra* is a widely-distributed species in sub-Saharan Africa, occurring in the mountain regions of East Africa (e.g., Kenya, Tanzania, Uganda and Ethiopia), as well as in southern Africa (e.g., South Africa, Namibia, and Zimbabwe) (Liu et al., 2009). In South Africa, the species is common, occurring in the Cederberg Mountains of the Western Cape, northern provinces of Gauteng and Limpopo, the eastern parts of South Africa from the coasts of KwaZulu-Natal and Eastern Cape provinces, to the interior including Eswatini and Lesotho (Germishuizen and Meyer, 2003). It is found at altitudes of 20 to 2440 m on damp slopes, along streambanks and forest margins (Goldblatt and Manning, 2000; Manning and Goldblatt, 2012; Poolely, 1998). As a record of the modern environment specifically, the upper part of the C4 sediment core collected in 2011 near the Mtentu River (see Fig. 9 in Fisher et al., 2013) showed that only 20% of its pollen spectra was represented by *Artemisia* and other Asteraceae pollen. Such a high abundance of *Artemisia* pollen as detected at Waterfall Bluff is rare in southern Africa (pers. comm. Louis Scott). An exception is the alluvial sequence of Craigrossie, in the eastern Free State, where ~50% *Artemisia* pollen was recorded in a single sample and interpreted as a signal of a local *Artemisia* stand (Scott, 1989, pers. comm.

Louis Scott). *Artemisia afra* (“umhlonyane” to the amaPondo people) is also one of the most widely used medicinal plants in South Africa for treating tuberculosis and malaria, and a wide range of illnesses such as coughs, colds and fevers, heartburns or hemorrhoids (e.g., Kepe, 2007; Masoko and Nxumalo, 2013; van Wyk and Gericke, 2000). It is also a popular South African food and is used as a natural insect repellent (Roberts, 1990). Therefore, we cannot exclude the possibility that *Artemisia* plants were brought into the site by humans (Leroi-Gourhan and Allain, 1979). These results would thus further suggest that plant-gathering strategies at Waterfall Bluff were not restricted to fuel-wood collection, but species for medicinal purposes were also targeted (Table 2).

The grass phytolith concentration at Waterfall Bluff decreases from MIS 3 to the Early Holocene. But what was the agent of deposition of the grass phytoliths? We consider two possible scenarios. First, it is plausible to consider that grasses were growing naturally onsite during MIS 3 favoured by damp soil conditions as indicated by the presence of algal remains (Fig. 5) and low human occupation (Fisher et al., 2020). Alternatively, grasses could have been deliberately introduced by past inhabitants for many different purposes like lighting fires (van Wyk and Gericke, 2000), bedding (Wadley et al., 2020), or even partially attached to the wood bark used for fuel (e.g., Esteban et al., 2017b). However, at this stage of the investigation it is difficult to rule out any of these scenarios. Sedge phytoliths and pollen also occur throughout the Waterfall Bluff deposits but are more abundant at the beginning of the LGM and during the first and last occupation episodes of the Holocene sequence. Sedges have been reported at several archaeological sites in South Africa and interpreted as brought in by humans (Backwell et al., 2014; Esteban et al., 2020a; Henderson et al., 2006; Murungi, 2017; Sievers, 2006; Wadley et al., 2011, 2016). It is, therefore, plausible that its presence at Waterfall Bluff indicates the use of this plant by its former inhabitants, which could have been used for a variety of purposes, such as weaving and matting (van Wyk and Gericke, 2000).

Our record can also provide a time window for assessing plant availability and gathering strategies by past people in coastal Eastern Mpondoland. The woody taxa identified in the MIS 3 and LGM deposits are currently found in a variety of vegetation communities such as deciduous, bushveld and riparian forests as well as on rocky outcrops in both grasslands and river valleys (Table 2). The presence of species that occur in extant coastal forest communities (MIS 3, *Cassipourea* sp. [possibly *flanaganii*] and *Ficus* sp. [possibly *bizanae*]; LGM, *Cordia caffra*; Table 2) indicates that past inhabitants

at Waterfall Bluff were collecting wood along the coast during glacial phases. Evidence for shellfish foraging and marine fishing during the same time periods have linked the occupants of the site to the coast during MIS 3, the LGM, and LGIT (Fisher et al., 2020). The charcoal evidence strengthens those people's relationship to the coast and increases the breadth of their activities known to have occurred there. However, woody species that occur in inland forests and dry bushveld, which also could have occurred in rocky and forested areas above the current coastal cliffs at Waterfall Bluff were identified as well during the MIS 3 (*Canthium inerme* and *Dombeya rotundifolia*), LGIT (*Ximenia caffra*) and Early Holocene (*Kirkia wilmsii* and *Grewia flavescens*). Overall, these results not only indicate the diverse plant availability surrounding Waterfall Bluff over time, but also that people were exploiting a relatively large variety of vegetation types and landscapes, from coastal regions to the interior plateau above the current coastal cliffs.

5.3. Glacial/interglacial environmental changes in Eastern Mpondoland

5.3.1. Marine Isotope Stage 3

South African MIS 3 palaeoenvironments were characterised by relatively abrupt changes in temperatures and precipitation (e.g., Huber et al., 2006), and cool conditions seemed to have dominated from around 40 ka (see the discussion in Scott and Neumann, 2018). Marine records offshore eastern South Africa are interpreted to show elevated precipitation over the coastal region (core CD154-10-06 P, Simon et al., 2015b), with sea surface temperatures (SSTs) around 3 °C lower than present (core MD96-2048, Caley et al., 2011). As it is debated which part of the signal recorded in offshore marine archives was transported by the strong Agulhas Current from equatorial areas southwards, for example towards the Mpondoland coast, local coastal archives such as the one presented here have a high significance. At Waterfall Bluff, the enriched δD_{wax} values of the MIS 3 deposits suggest low rainfall conditions. Northward shifted and intensified westerlies during times of extended sea-ice coverage around Antarctica likely caused a north-eastward displacement of the Southern Indian Ocean Convergence Zone (SIOCZ, Cohen and Tyson, 1995; Cook et al., 2004). In turn, this was associated with a reduction in total rainfall and also a reduction in rainfall (summer) seasonality. Previous research results suggest that regional hydrology during the Pleistocene was influenced by changes in orbitally modulated insolation (Partridge et al., 1997; Simon et al., 2015). Reduced local summer insolation during MIS 3

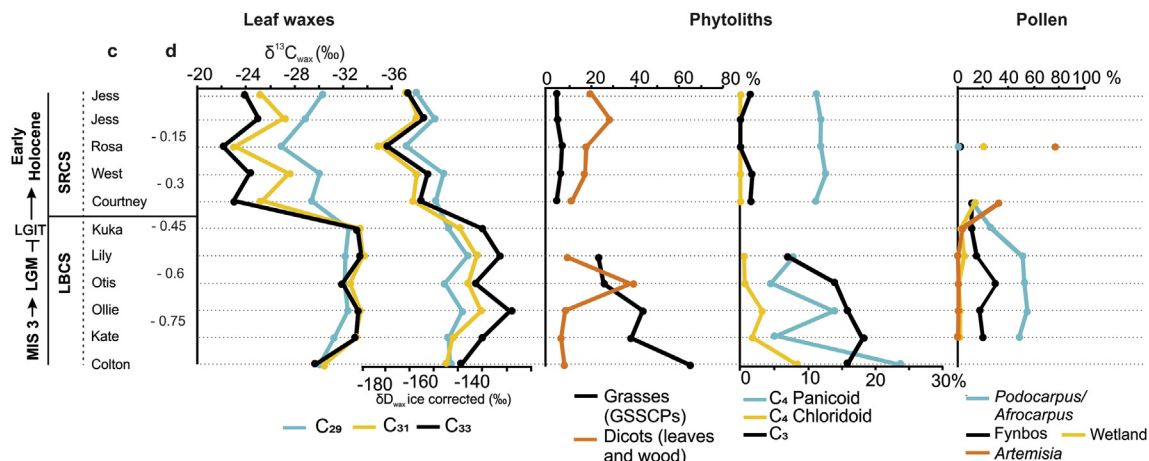


Fig. 8. Composite diagram of the Waterfall Bluff vertical transect sequence. The diagram shows the most significant leaf wax, phytoliths and pollen results discussed in this study. a, Chrono-geologic/climatic period; b, Stratigraphic provenance; c, Depth below the surface (meters).

would thus have resulted in low precipitation (Caley et al., 2018; Partridge et al., 1997; Schefuß et al., 2011a). Less intense seasonal rainfall at this time is also reflected in the δD_{wax} record of the Mfabeni peatland (Miller et al., 2019) and the pollen-based Central and Eastern Precipitation stack (Chevalier and Chase, 2015). The presence of Fynbos species in the phytolith and pollen record and good representation of C_3 Pooideae grass phytoliths from Waterfall Bluff supports the occurrence of winter rain and shrubland vegetation around the site, which are also edaphically and climatically limited (dystrophic soils and cool climates) and characterised bioclimatically by predominantly winter rainfall. Their representation therefore supports the δD_{wax} interpretation of low total rainfall and a low seasonality (Fig. 8). The main rainfall season likely was during winter.

The low $\delta^{13}C_{wax}$ values indicate the dominance of C_3 vegetation around Waterfall Bluff during MIS 3. As indicated above, C_3 grasses (cool growing season) are also well-represented at Waterfall Bluff at this time, as indicated by C_3 Pooideae grass phytoliths representing between 11% and 4% of the total grasses (Supplementary Table 1). This is unlike the current Panicoideae domain (Shackleton et al., 1991) which is reflected in the dominance of C_4 Panicoideae grass phytoliths as indicated by modern local analogues (i.e., the upper part of the C4 sediment core near the Mtentu River; see Fig. 9 in Fisher et al., 2013). At Waterfall Bluff, one third of the pollen spectra during this time interval comprises herbs and shrublets (Fig. 6), with a strong presence of fynbos taxa, e.g. Ericaceae, Passerina and Stoebe/Elytropappus. These taxa might indicate low temperatures as also evidenced at Vankervelsvlei at the southern coast of South Africa (Quick et al., 2016). Plant taxa characteristic of a diversity of habitats such as rocky grasslands (i.e., *Canthium inerme*) as well as deciduous bushveld (*Olea* sp.) and coastal forests (i.e., *Ficus* sp. [possibly *bizanae*] and *Cassipourea* sp. [possibly *flanagani*]) (Table 2) are also represented at Waterfall Bluff. Similarly, dry and hygrophilous grasslands might have also been present, as indicated by the presence of Chloridoideae (C_4 xerophytic) and Panicoideae (C_4 mesophytic to helophytic) grass phytoliths, probably interspersed with the forests and bushveld vegetation communities (Figs. 5 and 7). Grasslands would have not dominated the local environments as indicated by their low pollen representation (Fig. 8).

During glacial MIS 3 low temperatures and reduced summer insolation (Caley et al., 2018; Partridge et al., 1997; Schefuß et al., 2011b) would have reduced the levels of evapotranspiration, leading to higher moisture availability. Under these conditions, afrotemperate vegetation may have benefitted, and the high frequencies of *Podocarpus/Afrocarpus* and other tree pollen at Waterfall Bluff indicate a local vegetation where afrotemperate elements seem to have been well-established (Figs. 5 and 7). Our finding of *Podocarpus/Afrocarpus* forests along the South African East coast during MIS 3 seems to be in agreement with other terrestrial environmental records such as the Mfabeni peatland further (~400 km; Fig. 1a) north from Mpondoland (Finch and Hill, 2008). Still, if the high frequencies of *Podocarpus/Afrocarpus* pollen (49–56%) at Waterfall Bluff depict the presence of extensive podocarp forests (following Coetzee, 1967), what was the pollen source area? Bathymetry data from four existing datasets [shown in Fisher et al., 2020; derived from South African Navy hydrographic chart SAN 130; the ETOPO1 – 1Arc-Minute Global relief Model of Amante and Eakins (2009) and Dingle et al. (1987), and archival data of the Council for Geoscience] estimates the position of the coastline to be ~3 km away from Waterfall Bluff during MIS 3. Submarine canyons linked to many modern river systems (e.g., Umzimvubu, Msikaba, Mtentu and Tezana rivers) in the area have been detected from these bathymetric data and during recent marine geoscience mapping of the seafloor near Waterfall Bluff

(Cawthra and MacHutchon, 2019, see Fig. 1 in Fisher et al., 2020). Since the mouth of the shelter points southward (Figs. 1–3), NNW and SE prevailing winds (Cawthra et al., 2012) could have deposited large amounts of airborne *Podocarpus/Afrocarpus* pollen from across the region, and especially from vegetation found on the exposed narrow continental margin. Thus, it is plausible that forests containing podocarps could have grown along river valleys and scarps on the exposed canyons formed by paleo-rivers along the Mpondoland exposed continental shelf. Here, they would have been protected from berg-wind fires (Geldenhuys, 1994), and perhaps also supported by soil moisture available along the active paleo-rivers.

However, since *Podocarpus/Afrocarpus* pollen can be over-represented due to the aerodynamic properties of the pollen, prevailing wind patterns and high pollen production (Coetzee, 1967), it is difficult to tell exactly in which direction these forest might have grown. For example, with the northward displacement of the westerlies at the time (e.g., Miller et al., 2019), we cannot ignore that prevailing westerly winds could have also transported *Podocarpus/Afrocarpus* pollen from further west towards Mpondoland. So where would have these *Podocarpus* trees been growing inland? Afrotemperate forests were not only restricted to coastal regions during MIS 3, as *Podocarpus* pollen has been recorded in the north-interior areas of South Africa, for example at Wonderkrater, indicating the presence of montane forests in the surrounding environments (Scott, 1982a, 1982b, 2016), or Tate Vondo (Baboolal, 2014). In the highveld of the Eastern Cape, the available data suggests that large *Podocarpus* forests seemed to have been absent in the highlands of Lesotho. At Grassridge rock shelter, in the high elevation grasslands of the Eastern Cape (~200 km East of Waterfall Bluff; Fig. 1a), for example, phytoliths indicate little woody vegetation under generally cool and dry conditions during MIS 3 (43–28 ka) (Ames et al., 2020). Likewise, in the Maloti-Drakensberg highlands of Lesotho northwest of Mpondoland, phytoliths and soil organic matter $\delta^{13}C$ values were interpreted to reflect cool and wet/humid conditions, and the dominance of woodlands and C_3 grasses (Stewart et al., 2016). Under these conditions, it does not seem plausible that large *Podocarpus* forests would have been present in the region. Further west, the Vankervelsvlei record on the southern coast (~400 km SW from Waterfall Bluff) shows a weak representation of afrotemperate forest taxa including *Podocarpus/Afrocarpus* during MIS 3 (Quick et al., 2016). Therefore, from the available evidence, it thus seems more plausible that the source of the *Podocarpus/Afrocarpus* pollen at Waterfall Bluff derives from forests growing along the exposed continental shelf of coastal Mpondoland.

In summary, our proxy data indicate low rainfall due to reduced summer rains resulting in lowered rainfall seasonality and winter as main rainfall season. Reduced summer insolation and low temperatures could have likewise reduced evapotranspiration resulting in higher relative moisture (Chevalier and Chase, 2016) favouring a mosaic of plant communities. These data are in contrast to the interpretation of increased rainfall from the marine archives which therefore might be overprinted by a signal from more equatorial areas transported southward by the Agulhas current. At Waterfall Bluff, MIS 3 palaeoenvironments seemed to have been characterised by the presence of open woodlands interspersed with dry and hygrophilous grasslands and bushveld vegetation perhaps on the hills above the actual coastal cliffs and *Podocarpus/Afrocarpus* forests along steep slopes of the river valleys and scarps along the exposed continental shelf in front of Waterfall Bluff, or from the interior and their pollen transported by the intensified westerly winds.

5.3.2. The Last Glacial Maximum

During the LGM, eustatic sea level dropped up to -125 m, drastically changing the coastal topography across most of South Africa (e.g., Cawthra et al., 2020, 2014; Clark et al., 2009; Fisher et al., 2010). In Mpondoland, the narrow continental shelf restricted coastline movements to ~ 8 km away from Waterfall Bluff (Fig. 1b; Fisher et al., 2020). During glacial periods, the expansion of the Antarctic sea ice resulted in an equatorward displacement of the southern westerlies leading to a northward expansion of the winter-rainfall-zone (e.g., Chase and Meadows, 2007). Offshore of Mpondoland, the Fe/K record from marine core CD154 17–17 K suggests high precipitation and cool conditions with SSTs of around $6-7$ °C lower than present (Simon et al., 2013). These results could support a model suggested by Engelbrecht et al. (2019) that found an increase in annual rainfall over eastern South Africa.

From MIS 3 to the LGM at Waterfall Bluff, the slight increase of fynbos elements and C_3 Pooideae grasses, low $\delta^{13}C_{wax}$ values and the decrease of C_4 Chloridoideae (Figs. 5–7; Supplementary Table 1) suggest the persistence –and perhaps the increase – of cold conditions in coastal Mpondoland. These results do not track the decrease of atmospheric CO_2 during the LGM (180–200 ppmv; e.g., Fischer et al., 1999), as under this condition C_4 grasses would have been favoured. Conversely, the high presence of *Podocarpus/Afrocarpus* and other forest taxa (62–64%) in the LGM deposits indicates the persistence of afrotemperate forests under low temperatures (fynbos elements and C_3 grasses) and low rainfall and low rainfall seasonality conditions (δD_{wax}) similar to the MIS 3 (Fig. 8). As inferred for MIS 3, the northward displaced southern westerlies during the LGM would have shifted the SIOCZ towards the northeast and suppressed summer rainfall in the coastal area stretching from Mfabeni to Mpondoland (Miller et al., 2019). Similarly, it is possible that the northward displacement of the southern westerlies during the LGM introduced pollen from regions west of Waterfall Bluff to the site. North of Mpondoland, at the Mfabeni peatland in KwaZulu-Natal, a peak of *Podocarpus* and Asteraceae pollen was also observed at the commencement of the LGM, followed by a decline until the end of the LGM (Finch and Hill, 2008). At Mfabeni, the δD_{wax} values also point towards a low rainfall intensity and/or high evapotranspiration and a low water table as a result of a northerly displacement of the southern westerlies during the LGM (Miller et al., 2019). At Strathalan B, in the highveld of Eastern Cape, relatively humid grasslands with swampy conditions were reconstructed for the beginning of the LGM. By ca. 21 ka when the site was abandoned, the pollen record indicates environments transitioning to colder and drier conditions (Opperman and Heydenrych, 1990). The profile of Vankervelsvlei on the South African south coast for example shows a gap in the pollen record from $\sim 27-8.7$ ka, which is interpreted to be the result of increased aridity (Quick et al., 2016) and correlated to a decrease in the Agulhas Current SSTs (Quick et al., 2016) and a sea-level lowstand (Cawthra et al., 2020). This scenario is consistent with reports of increased aridity at the Southern Cape during the Last Glacial Maximum (Chase and Meadows, 2007; Faith et al., 2019; Scholtz, 1986).

During the LGM, a precessional maximum should have resulted in higher precipitation (e.g., Simon et al., 2015). At Waterfall Bluff, the similar δD_{wax} and $\delta^{13}C_{wax}$ values and distributions from MIS 3 to the LGIT suggest that local summer insolation changes have not affected moisture availability in coastal Mpondoland during the Late Pleistocene. These results support previous studies, which proposed that precessional driven local insolation forcing was not controlling precipitation in South Africa during the Late Pleistocene (e.g., Chevalier and Chase, 2015; Miller et al., 2019; Schefuß et al., 2011a,b). Under these conditions, if *Podocarpus/Afrocarpus* forests were growing along the Mpondoland exposed continental shelf,

their survival must be related to their protection in the deep gorges from berg-wind fires (Geldenhuys, 1994) and low evapotranspiration favoured by cool conditions (fynbos elements and C_3 grasses) (Fig. 8). More importantly, incisions of numerous palaeo-rivers on the submerged continental shelf indicate active riverine runoff at the time, supporting the presence of freshwater to support hunter-gatherers as well as wetland vegetation in the surroundings (Coates-Palgrave, 2002), that is indicated by slightly elevated levels of *Typha* and Cyperaceae pollen and phytoliths at Waterfall Bluff (Fig. 8). Lastly, the proximity to the ocean could have favoured mist, providing relatively higher near-coastal soil moisture conditions for the development of forested vegetation along the ~ 8 km of exposed continental shelf. Alongside with *Podocarpus/Afrocarpus*, pollen of other forest trees like *Ilex* (max. 1.1%), *Salix* and Myrtaceae are also well represented during the LGM at Waterfall Bluff.

The identification of *Cordia caffra* in the charcoal record, which currently grows in coastal and riverine forests along the Wild Coast coastal belt and up to Mozambique, might depict the presence of forests that would have occurred either on the coastline or along the water courses situated on the ~ 8 km exposed continental shelf. Coastal forest belt expanded along the Mozambique coastline after ~ 8000 14C yr BP (Eeley et al., 1999; Lawes et al., 2007), and therefore, the presence of typical coastal forest taxa at the Waterfall Bluff record during the LGM deposits might be indicative of an earlier expansion of coastal belt forest elements south of the Mozambique coast. Nonetheless, this hypothesis is tentative and needs to be further tested. Finally, the presence of dicot leaf phytoliths in high frequencies indicates, on one hand, their intentional introduction by past inhabitants. On the other hand, their presence also supports the pollen and charcoal records by indicating the availability of trees and/or shrubs in the surroundings of Waterfall Bluff during the earliest LGM.

In summary, our data support the hypothesis of a survival of afrotemperate forests in coastal Mpondoland during the LGM and perhaps their expansion along the ~ 8 km of exposed continental shelf in front of Waterfall Bluff. However, more palynological data from other parts of the Waterfall Bluff sequence and from the region are needed to verify this hypothesis. Other woodland landscapes would have been also present in the surroundings of Waterfall Bluff, and although tentatively, coastal forests might have also occurred, and probably along the coastal ridges. Finally, our results are in support of the model suggested by Engelbrecht et al. (2019) of a relatively humid Eastern South Africa, perhaps as a result of low temperatures and low evapotranspiration (supported by our data) rather than an increase in precipitation (as indicated by the model simulations).

5.3.3. The Pleistocene – Holocene transition

The only LGIT deposit represented in the vertical profile here studied is LBCS Kuka (13,880–13,510 cal. BP to 13,470–13,130 cal. BP; Fisher et al., 2020), and potentially coeval with the Younger Dryas. While the leaf waxes show similar values over the LBCS deposits covering MIS 3 to the LGIT, an abrupt change in Waterfall Bluff's pollen record occurs in LBCS Kuka, with rapid decline of *Podocarpus/Afrocarpus* ($<20\%$) and *Elytropappus/Stoebe* pollen while Poaceae and Asteraceae—and other open land indicators, like Aizoaceae and Amaranthaceae—increase (Figs. 6 and 7). The contraction of *Podocarpus/Afrocarpus* forests at this time could be explained as a result of the progressive loss of continental shelf due to marine transgressions. However, the stratigraphic section that was sampled for this study is also missing deposits between 19 and 14 ka, which are now known to occur further inside of the rock shelter (see Fig. 5 and Table 1 in Fisher et al., 2020). Therefore, the rapid decline in afrotemperate forest elements may be artificial and future analysis will allow us to fill the gap in the results presented

here. Yet, the pollen signature may have been obscured by diagenesis as indicated by the high percentage of *varia* pollen (19%) noted in this deposit. Despite the small sample size of charcoal from the LGIT deposit, the identification of *Ximenia caffra* in LBCS Kuka, a tree that is currently restricted to more arid biomes of South Africa (Table 2), indicates that conditions might have been drier than at present, and probably in the neo-coastal peneplain. Nonetheless, the good representation of *Phragmites*-type pollen during these occupations reflects the persistence of wetland elements in the surroundings of Waterfall Bluff, and probably along the narrow strip between the current and the LGIT coastlines.

During the transition to the Holocene, the substantially depleted δD_{wax} values at Waterfall Bluff compared to the Pleistocene deposits suggests the intensification of summer rainfall along the eastern coast of South Africa with the retreat of the southern westerlies to higher latitudes. The retreat of the westerlies would have led to a switch from low rainfall amounts mainly during winter to stronger rainfall intensity mainly during austral summer (Miller et al., 2019, 2020). This was also detected in the data from the Mfabeni peatland (Miller et al., 2019), and correlates well with the Central and Eastern Precipitation stack of Chevalier and Chase's (2015). The enriched $\delta^{13}C$ values of plant waxes at Waterfall Bluff, indicates a strong contribution of waxes from C_4 plants, which could be explained by the expansion of specific C_4 plants (e.g., Chloridoideae and Panicoideae grasses, sedges and palms) in humid edaphic conditions (Fig. 8). Alternatively, the closer vicinity of the coast at the time might have had an influence via a higher contribution of sea spray to the site. Many C_4 grasses are salt-tolerant species (e.g., Bromham and Bennet, 2014) and could have thus inhabited the more salt-affected areas around the site at this time. Phytoliths from sedges (Cyperaceae) are well represented in these deposits and, since Poaceae phytoliths (GSSCPs) are largely absent, it is possible that ELONGATE morphotypes with decorated margins (i.e., Elongate columnar, crenate, dentate, echinate, ligulate, sinuate), which were recovered in very high numbers, belong to graminoids other than grasses, and perhaps to sedges. Wetland pollen elements (i.e., *Typha* and Cyperaceae) also expanded during this time, and together with the phytolith results and $\delta^{13}C$ values, indicate locally warm and humid conditions in coastal Mpondoland during the Early Holocene (Fig. 8). These results are in agreement with an expansion of wetlands and in sync with rising sea levels in the surrounding areas of Waterfall Bluff and as per seismic records from other now-submerged areas to the north and south (e.g., Bosman, 2012; Cawthra et al., 2020, 2012). Finally, the Early Holocene taxa identified through the charcoal study completes the reconstruction of the surroundings of the site indicating the presence of coastal forests, forest margins and valley bushveld vegetation. Coastal dune elements, probably more abundant and closer to the site at this time due to the inland transgression of the seashore, were also represented by the presence of *Phoenix* and *Hyphaene* pollen (probably *P. reclinata* and *H. coriacea*), which are also C_4 plants.

At Waterfall Bluff, although the pollen record was affected by oxygenation resulting in high percentage of crumpled, unidentifiable pollen, the record suggests more open environments (i.e., an increased in Poaceae and decrease in *Podocarpus/Afrocarpus*). Conversely, the Mfabeni peatland shows a rapid increase in *Podocarpus* pollen of up to 60% during the Early Holocene, which Finch and Hill (2008) interpreted as showing the expansion of *Podocarpus* forests depicting moister and cooler conditions (Finch and Hill, 2008). Similarly, palynological results from Lake Eteza at 10.2 ka show a dominance of woody vegetation (podocarps) and wet conditions (Neumann et al., 2010). The increase of atmospheric CO_2 (e.g., Fischer et al., 1999) and reduced summer insolation (e.g., Partridge et al., 1997) with the beginning of the Holocene could

have favoured, among other factors, the expansion of forests as it is observed at Mfabeni and Lake Eteza, north of Mpondoland. This is not reflected in our proxy record and thus it is plausible that the decrease of pollen of *Podocarpus/Afrocarpus* at Waterfall Bluff since the LGIT was triggered by high temperatures and increasing evapotranspiration what could have reduced relative humidity. The loss of terrestrial habitats due to the progressive inland transgression of the shoreline, which was situated as closed as 1.5 km from Waterfall Bluff at this time (Fig. 1) could have also accounted for this. In the same way as for the MIS 3 and the LGM, the westerlies could have influenced pollen deposition at Waterfall Bluff. It is thus plausible that even though *Podocarpus* forests could have occurred in the regional environments, the southward displacement of the westerlies could have prevented the deposition of their pollen on site. *Podocarpus* forests could have still been present in the local and regional environments, in the valleys across the adjacent plateau that crossed Mpondoland from the interior to the coastal areas, as it is observed today. Indeed, *Podocarpus/Afrocarpus* pollen is also detected in the C4 core sequence, from the Middle Holocene to the present, albeit in low frequencies (<5%, see Fig. 9 in Fisher et al., 2013). In these conditions, we suspect that the orientation of the westerlies and low wind strength (Miller et al., 2020) could have all prevented the deposition of *Podocarpus/Afrocarpus* pollen at Waterfall Bluff during the Early Holocene.

In summary, the Waterfall Bluff record during the Early Holocene points towards local environments characterised by the presence of open landscapes and edaphic habitats with bushveld vegetation probably protected in rocky outcrops in the coastal peneplain, along with coastal forests occupying the coastal dunes adjacent to the seashore. This record adds local environmental information for the beginning of the Early Holocene in Eastern South Africa and along with several other palaeoenvironmental records points towards an overall increase in rainfall, a switch from winter to summer rain predominance, open and mesic landscapes and higher temperatures.

6. Conclusions

The continental shelf in the Mpondoland region of South Africa's eastern seaboard is narrow (~8 km wide) providing the necessary geological context to track plant exploitation and environments across glacial and interglacial phases. Archaeological evidence shows that hunter-gatherers visited Waterfall Bluff regularly since late MIS 3, at least. With good preservation of biotic and abiotic palaeoenvironmental proxies, the site provides an opportunity to study past hunter-gatherer plant foraging strategies and reconstruct their surrounding environments in a coastal context. Here, we present initial results of a multi-proxy study that combines pollen, phytoliths, charcoal, macrobotanical remains and plant wax carbon and hydrogen isotopes from the same archaeological site in South Africa to investigate interactions between hunter-gatherer plant-gathering strategies and environmental changes from MIS 3 to the Early Holocene.

The diversity of the tree species identified in the charcoal record at Waterfall Bluff from MIS 3 to the Early Holocene indicates a selective collection of plant species for different purposes, which could have been used not only for fuelwood, but also for medicinal purposes, among others. The use of medicinal plants during the early Holocene at Waterfall Bluff is also implied by the high occurrence of *Artemisia* pollen. The charcoal record indicates that the past inhabitants of Waterfall Bluff also collected wood from coastal vegetation communities, during both glacial and interglacial phases, and this finding supports other lines of evidence for coastal exploitation at Waterfall Bluff (Fisher et al., 2020).

During MIS 3 (ca. 37 ka) and the LGM (from ca. 23 to 19 ka) at

Waterfall Bluff, the climate was likely characterised by low total rainfall resulting in low rainfall seasonality. Winter rain and low temperatures resulted in an expansion of fynbos elements and C_3 grasses. Low glacial temperatures could have reduced evapotranspiration resulting in higher relative humidity (i.e., higher moisture availability) (Chevalier and Chase, 2016) favouring a mosaic of plant communities. These might have been characterised by the presence of open woodlands interspersed with dry and hygrophilous grasslands and bushveld vegetation perhaps on the hills above the coastal cliffs, *Podocarpus/Afrocarpus* forests along steep riverine slopes and scarps along the exposed continental shelf in front of Waterfall Bluff, and coastal forests along the seashore. *Podocarpus* forests could have also occurred in the interior regions along scarps and gorges where they would have been protected from wind and fire, and transported to Waterfall Bluff by strong westerlies during MIS 3 and the LGM.

During the LGIT, ca. 14 to 13 ka, the environmental conditions at Waterfall Bluff changed with evidence for forest retreat and open land indicators most likely in relation to post-LGM marine transgression and the retreat of the southern westerlies to higher latitudes leading to increased total rainfall and higher rainfall (summer) seasonality. With the transition to the Holocene, from ca. 11 to 10 ka, our records indicate the persistence of summer rainfall conditions with the decline of afrotemperate forests and fynbos elements and the expansion of local environments characterised by the presence of open landscapes and mesic habitats with bushveld vegetation probably protected in rocky outcrops in the coastal peneplain, along with coastal forests occupying the coastal dunes adjacent to the seashore. This record thus adds local environmental information for the beginning of the Early Holocene in eastern South Africa and along with several other palaeoenvironmental records points towards an overall increase in rainfall, open landscapes and higher temperatures.

The proxy-data presented here not only indicate that landscapes surrounding Waterfall Bluff were diverse over time, but also that people exploited a large variety of vegetation types and landscapes, from coastal regions to the interior plateau above the current coastal cliffs. This multi-proxy study shows that archaeological records such as Waterfall Bluff are good indicators of local environments but also enables to evaluate climatic conditions, vegetation changes and plant foraging strategies. The Waterfall Bluff archive, although discontinuous and currently sampled at relatively low resolution, provides a framework to support future palaeoenvironmental and palaeoclimatic work in Mpondoland and in coastal eastern South Africa, a rather unexplored region where the Pleistocene – Holocene transition is inadequately covered by existing records.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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