



# Cooked starchy food in hearths ca. 120 kya and 65 kya (MIS 5e and MIS 4) from Klasies River Cave, South Africa

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## ABSTRACT

Plant carbohydrates currently constitute 55–80% of the modern human diet (FAO and WHO, 1997) and some of today's key global health issues are associated with excessive carbohydrate consumption. However, starch carbohydrate is still a poorly understood element of modern human diet and our past starch diet may provide insights for future research. Despite an archaeological narrative that links our early hominin ancestors to a diet that is rich in roots and tubers, there is little deep time archaeological evidence of human plant starch consumption. Geneticists hypothesise that the duplication of starch digestion genes in early *Homo sapiens* (~300 kya), is an adaptive response to an increased starch diet. Here we offer the earliest evidence of identified fragments of charred starch plant tissue (parenchyma) from cave and rock shelter hearths dated to Marine Isotope Stage (MIS) 5e and MIS 4, from the Middle Stone Age (MSA) site of Klasies River main site, South Africa (34.06°S, 24.24°E).

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## 1. Introduction

In this paper, we examine macrofossil evidence for the cooking and consumption of starchy plant tissues by humans at Klasies River from ca. 120 kya (or MIS 5e) and 65 kya (or MIS 4). We recovered and identified charred parenchyma from layers stratified within intact hearth features, with sample locations guided by the results of previous micromorphological analyses. Cooked vertebrate and shellfish remains have been identified in these hearths suggesting that the diet of these early modern humans exploited the diverse range of foods available around Klasies River that included both protein and carbohydrates. Our study is relevant to recent genetic and biological research into the human carbohydrate diet. This research has led to a hypothesis that *Homo sapiens* adapted to increased levels of starch as part of an omnivorous diet (Perry et al., 2007; Lazaridis et al., 2014; Inchley et al., 2016). Our

findings provide the archaeological evidence that has been previously lacking in support of this hypothesis. The combination of archaeobotany, micromorphology, organic petrology and molecular data has provided exceptional micro-contextual evidence and given further insights into early cooking and dietary activities.

## 2. Klasies River main site

The Klasies River main site (34° 06' 29" S, 24° 23' 24" E) is located on the Tsitsikamma coast between Port Elizabeth and Plettenberg Bay (Fig. 1).

The complex of caves and shelters that comprise the Klasies River main site is a well-documented Middle Stone Age (MSA) site in South Africa. The MSA occupation sequence spans at least 60,000 years, with further Later Stone Age deposits (Singer and Wymer, 1982).

The main site preserves around 21 m of deposits that were first substantially excavated by Singer and Wymer (1982), and thereafter by Deacon and Geleijnse (1988) who focussed on sampling small areas off the various sections left by Singer and Wymer. Their

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collective works have significantly enhanced the understanding of the stratigraphic sequence of Klasies River and its wider relevance on Middle Stone Age behavior and ecology. Wurz started a new phase of excavation in 2015, following the same protocols as those established by Deacon (Wurz et al., 2018). Klasies River main site has now produced evidence of more than 50 human fossil elements, representing mainly adults across all MSA stages but primarily from Marine Isotope Stage 5 (especially MSA II) (Grine et al., 2017). Some of these early remains are associated with ‘modern’ characteristics whereas others display more archaic elements and a distinct degree of sexual dimorphism, as one might perhaps expect for such early populations (Grine et al., 2017; Smith et al., 2017). The human remains are associated with abundant traces of occupation. These MSA sequences include indications of exploitation of ochre and evidence for complex chaîne opératoire of technologies such as those of Howiesons Poort (Wurz, 1999, 2008, 2013; Deacon and Wurz, 2005).

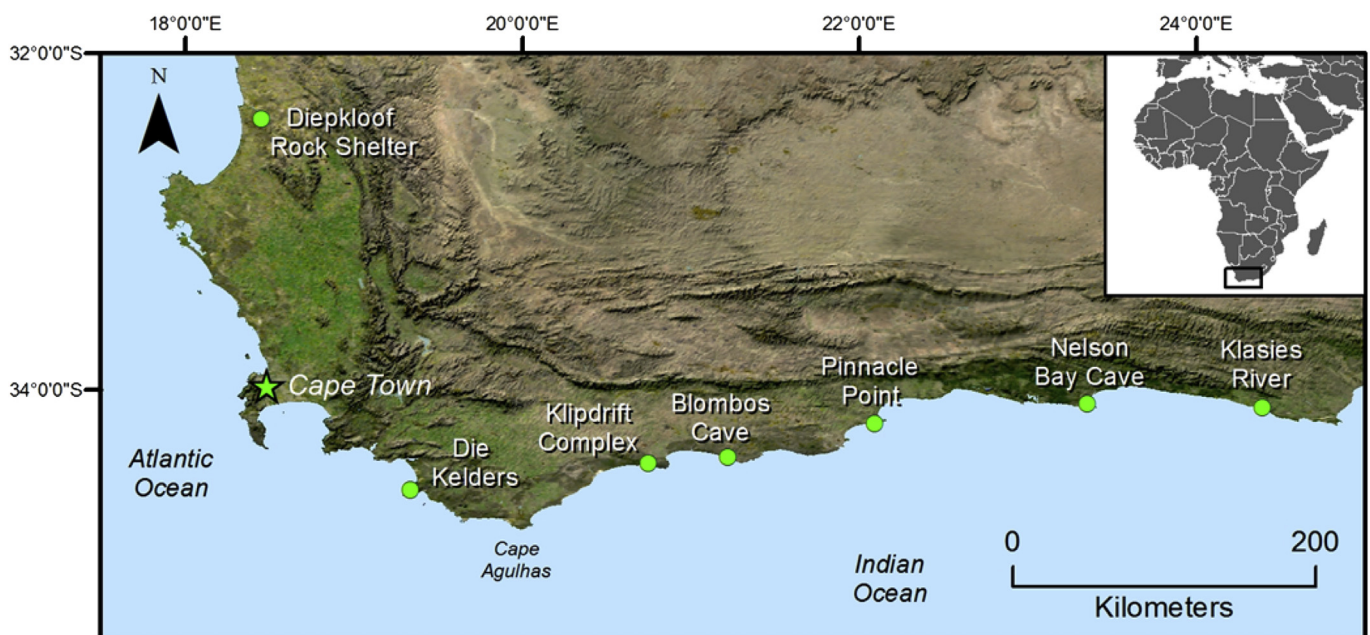
The MSA is defined as starting ~300 kya and continuing to ~40–22 kya, depending on the area investigated (Wurz, 2013; Wadley, 2015). In South Africa, the MSA is further defined by changes in lithic techno-complexes. The techno-complexes at Klasies River coincident with the phases researched in this paper are MSA 1 and Howiesons Poort. MSA 1 is a techno-complex of regular quartzite blades and elongated points. The Howiesons Poort is also a blade technology but of smaller dimensions and a wider range of raw materials. In addition, the blanks are retouched into geometric backed and notched artefacts (Wurz, 2013). Our sample from Cave 1 comes from the lower MSA 1 layers of the Light Brown Sand (LBS) member in the Witness Baulk. The Witness Baulk remained after the Singer and Wymer excavations in Cave 1 (Fig. 2) (Deacon and Geleijnse, 1988). The sample from the Witness Baulk corresponds broadly to level 38 of the Singer and Wymer excavations (Deacon and Geleijnse, 1988). The sample from the middle section of the Howiesons Poort phase in Cave 1A equates approximately to layers 17–15 excavated by Singer and Wymer (Fig. 2) (Singer and Wymer, 1982).

These MSA 1 layers equate to MIS 5d/e. This age estimation is based on serial  $\delta^{18}$  oxygen measurements of *Turbo sarmaticus opercula* (Loftus et al., 2017), a TL-OSL age of  $106.8 \pm 12.6$  (Feathers,

2002) and a U-Th date of  $108.6 \pm 3.4$  (Vogel, 2001). The Howiesons Poort sample comes from the uppermost part of the Cave 1A sequence referred to as layers 21–10 by Singer and Wymer (1982) and the Upper member by Deacon and Geleijnse (1988). The Howiesons Poort phase is associated with MIS 4 as indicated by a U-series date of  $65.6 \pm 5.3$  (Vogel, 2001) and a single grain OSL date of  $63.2 \pm 2.7$  (Jacobs and Roberts, 2017).

Both the MSA 1 and Howiesons Poort phases are related to periods during which relatively open environments prevailed. The large mammal faunal and microfaunal assemblage of these periods contain more grazers than browsers (Klein, 1976; Van Pletzen, 2000), and this is supported by the microfaunal evidence (Avery, 1987; Hillestad Nel et al., 2018), suggesting an emphasis upon grassland within the environmental mosaic. In the MSA 11 layers intercalated between the MSA 1 and Howiesons Poort phases, large mammal fauna and microfauna are suggestive of closed bush environments (Wurz et al., 2018).

During the Middle Stone Age occupation of Klasies River the diets of hunter-gatherers included significant amounts of vertebrate and shellfish (Klein, 1976; Thackeray, 1988; Van Pletzen, 2000). That starchy plants featured as part of the diet of the hunter-gatherers at Klasies had been anticipated by Deacon “A survey of remains of food plants from archaeological contexts in South Africa shows that geophytes, primarily corms and bulbs, were a major food resource.” (Deacon, 1993: 86). Geophyte gathering has been documented directly from well-preserved contexts dating to 30,000 years ago and indirectly through the context and association of carbonised remains in sites dating to the beginning of the Late Pleistocene more than 100,000 years ago (Deacon, 1993). Klasies River main site is situated within the Greater Cape Floristic Region. The region includes fynbos, renosterveld and karoo vegetation and is the world’s foremost region of geophyte diversity (Proches et al., 2006). In the immediate vicinity of the cave there is a mosaic of subtropical thicket, coastal dune thicket, Southern Cape Afrotemperate forest, and littoral vegetation, with fynbos elements (van Wijk et al., 2017). Roots and tubers are abundant in this varied biome and could have provided a consistent year-round source of energy (Bergh et al., 2014; De Vynck et al., 2016; Singels et al., 2016). The rich diversity of



**Figure 1.** Klasies River main site one of the key MSA sites on the Cape Coast of South Africa (Image: Magnus Haaland and reproduced with his kind permission).

geophyte species in the Cape region is attributed to the low incidence of extinction due to relative climate stability (Bergh et al., 2014). Klasies River provided an optimum sampling site to research perennial starchy plant processing and consumption.

### 3. The evidence for starch consumption

The earliest proposed inclusion of plant starch in the hominin diet is associated with the evolution of larger brains and bipedalism in early hominins. These morphological changes have been attributed to a dietary shift from high-volume, low energy fibrous forest foliage to a high energy, lower volume diet found in savanna and wetlands (Aiello and Wheeler, 1995). Increased amounts of meat and starchy underground storage organs (USO), rather than leaves and stems that are high in indigestible fiber, would have been more digestible and metabolically less expensive for australopiths and early habilines (4–2 million years ago), providing the energy for these key morphological changes (Aiello and Wheeler, 1995).

The ability to cook allowed for a step-change in diet quality and, it is argued, accelerated the rate of evolution within *Homo erectus* (Aiello and Wheeler, 1995; Wrangham et al., 1999; Aiello and Key, 2002; Wrangham, 2009). Cooked starchy plants would have provided a source of pre-formed glucose, essentially pre-digested foods, offering greatly increased energy availability for the brain, red blood cells and developing fetus (Hardy et al., 2015). Between two million and 500 kya, the cranial capacity of *H. erectus* doubled, their body size increased, particularly in females, and their teeth reduced in size; it is argued that the energy for these key morphological changes came in particular from cooked plant starches (Aiello and Key, 2002; Carmody and Wrangham, 2009; Wrangham, 2009; Hardy et al., 2015).

The dietary narrative for Neanderthals has, until recently, however, indicated that they were primarily a carnivorous archaic human species (Richards et al., 2000). But recent evidence indicates that Neanderthal dietary choices were determined more by climate and latitude, with DNA and starch grain evidence from fossilised dental calculus suggesting that Neanderthals adapted their diet to the local environment. While the diet of populations in higher latitudes appears to be meat dominated, Neanderthals from the Iberian Peninsula and across the Mediterranean were possibly consuming a wider plant diet with alternative sources of protein (Weyrich et al., 2017; Power et al., 2018). Neanderthals in Gibraltar exploited pine nuts and olives (Barton et al., 1999), while

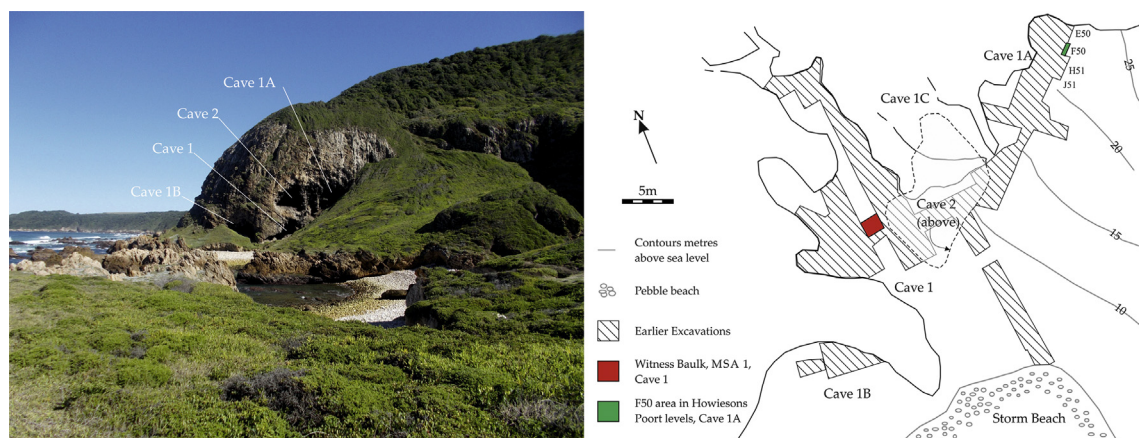
excavations at Kebara Cave, Israel have produced significant macro-remains. The starchy plants being consumed were grasses, including corms and seeds of wild barley (*Hordeum spontaneum/bulbosum*) and wild oats; legumes such as wild peas (*Pisum fulvum* and *Lens* sp.); pistachios (*Pistacia* sp.); and starchy underground storage organs such as bulbs and tubers (*Bellevialia* sp., Liliaceae and *Cyperus* sp., Cyperaceae) (Lev et al., 2005). At Amud Cave, Israel, phytolith evidence supports the inclusion of figs and starch palm hearts in the Neanderthal diet (Madella et al., 2002). This evidence is further supported by starch granule evidence from dental calculus indicating both grass seed and underground storage organ plant consumption (Henry et al., 2014).

#### 3.1. The evidence for starch consumption within anatomically modern humans

Evidence for starch consumption by anatomically modern humans (AMH) in the MSA, however, has hitherto relied upon starch granules captured within fossilized dental calculus and tools from the MSA sites of Klasies River and Blombos Cave, South Africa. While there is evidence for grass and USO starch granules, some of which were damaged, none showed conclusive evidence for cooking (Henry et al., 2014). So far as we are aware, deep time macrofossil evidence for cooked starchy roots and tubers in this time period remains elusive.

Much of archaeobotanical research conducted in MSA sites across South Africa has been directed at environmental reconstruction from charcoal and pollen notably as at Diepkloof (Cartwright, 2013), Elands Bay Cave (Parkington et al., 2000) and Sibudu (Allott, 2006). Phytoliths have been used to reconstruct the environment and the use of plants as fuel in the hearths at Pinnacle Point, Cave 1B (Albert and Marean, 2012; Esteban et al., 2018). At Sibudu Cave, layers of sedge, with rhizomes, were identified through micromorphology and charred macro remains in layers of bedding (Goldberg et al., 2009; Wadley et al., 2011). Sedge rhizomes have also been identified as potential food at Sibudu (Sievers and Muthama Muasya, 2011).

Tools for foraging are equally rare in the archaeological record. Ethnographic records indicate that wooden digging sticks are recurrently used for harvesting tubers. Re-analysis of digging sticks and digging stick weights, comparable with those used by San Bushmen, have been found in 35–40 thousand year old levels at Border Cave, South Africa. These foraging tools offer evidence of regular root and tuber harvesting (d'Errico et al., 2012). More direct



**Figure 2.** (Left) The main site at Klasies River (Cave 1A and Cave 1B are rock shelters). For scale: Cave 2 is maximally 8 m in height from the cave floor to ceiling and 18 m asl x 10 m wide (Singer and Wymer, 1982) (Image: C. Larbey) (Right): Main site plan shows sample locations. The MSA1 sample was located on the southern section of the Witness Baulk and the Howiesons Poort sample site was located in F50 (Plan: C. Larbey and D. Redhouse).

evidence is offered by the discovery of stores of dried bulb, tuber and corm remains in dry parts of caves such as Melkhoutboom Cave, Scott's Cave, Highlands Rockshelter and Strathalan B Cave (Deacon, 1976, 1993, 1995; Opperman, 1996) and would suggest that hunter-gatherers of the Later Stone Age may have included roots and tubers in their diet.

There is an increasing body of evidence from the rest of the world indicating that late Pleistocene, Epi-Palaeolithic and Mesolithic hunter-gatherers extensively processed, cooked and ate roots and tubers, grass seeds and arboreal fruits such as chestnuts, walnuts and acorns. The apparent perennial consumption of roots and tubers is in evidence across time and latitudes: the recovery of charred seeds and tubers dated to 60–50 kya from Medjedbebe in the Northern Territory of Australia (Clarkson et al., 2017); charred fragments of yams and taro from Niah Cave, Borneo in Southeast Asia (Barton and Paz, 2007; Barton et al., 2016); charred roots and tubers from the Upper Palaeolithic Dolní Věstonice II, Czech Republic; the earth ovens of Canada and America provide evidence for the cooking of camas lilies on a year-round basis (Thoms, 2008; Lyons and Ritchie, 2017); and importantly, the pre-agricultural discovery of bread-making from grain and tubers from the Natufian site of Shubayqa I, Jordan 14.4 kya (Arranz-Otaegui et al., 2018).

These data suggest that the modern human starch diet was not just a feature of the advent of agriculture, and that starchy plant foods had an important role in the diet of hunter-gatherers across a number of widely differing environments.

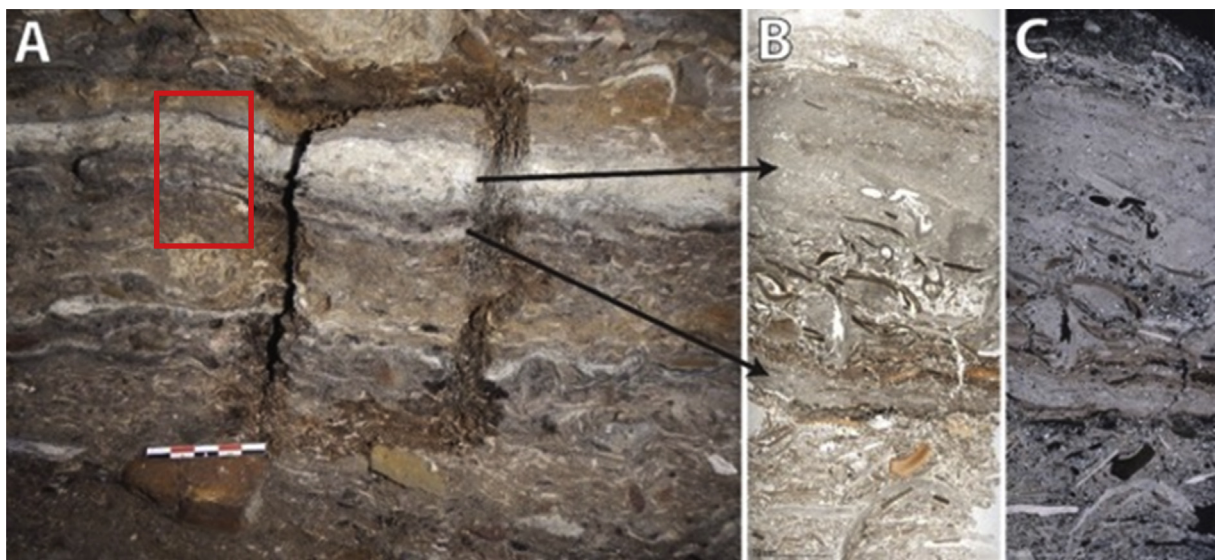
That early humans consumed starchy foods may be inferred from recent research into genetics and human biology. The largest area of genetic copy number variation (cnv) in the human genome is connected with human starch digestion (Carpenter et al., 2015). The gene AMY1 encodes the protein amylase in human saliva that initiates the process of hydrolysing starch into disaccharides and trisaccharides (simple sugars), the process is then completed in the small intestine with AMY2 amylase expressed in the pancreas. While great apes and archaic human species such as Neanderthals and Denisovans carry the diploid copy number of two AMY1 genes (Prüfer et al., 2014), in the

human lineage, the amylase genes have uniquely expanded, with AMY1 copy numbers varying between 2 and 20 (Perry et al., 2007; Lazaridis et al., 2014; Prüfer et al., 2014). A high read depth analysis of an 8000-year-old Mesolithic European hunter-gatherer indicated a high AMY1 cnv of 13, suggesting that adaptation to a higher starch intake preceded the advent of farming (Lazaridis et al., 2014). Further research has shown this starch adaptation to have occurred early in human evolution, c. 300,000 years ago in Africa and to have post-dated the human lineage divergence from Neanderthals and Denisovans (Inchley et al., 2016). While further insertions and deletions have occurred in populations after their dispersal out of Africa, the original duplication raised the human ancestral copy number of our salivary amylase gene from two copies to six copies (Inchley et al., 2016). Further, these gene copies are not blind, but are active in specific response to a starch diet (Falchi et al., 2014).

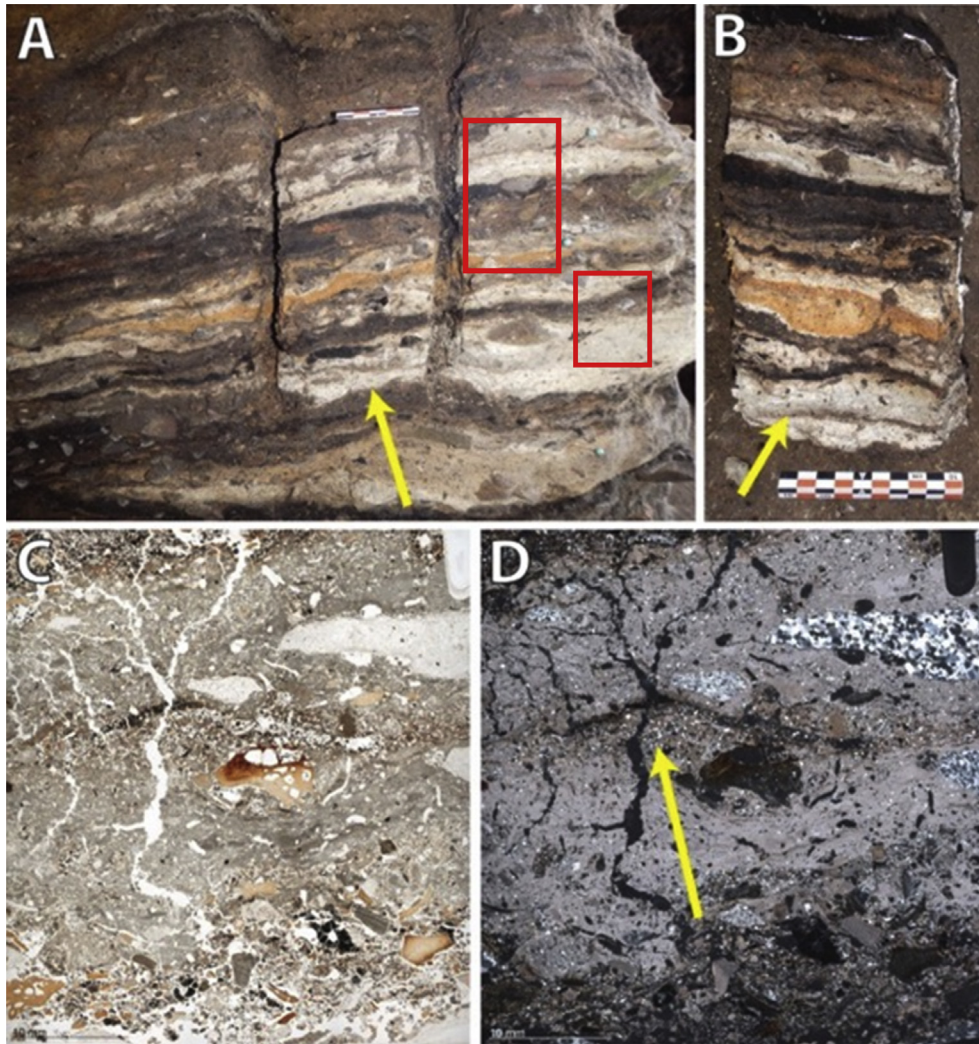
#### 4. Cooking and hearths

Only humans cook, and cooking is considered to have been a turning point in human evolution. Cooking makes food more digestible and in starchy plant foods such as roots and tubers, cooking pre-digests the starch turning it into preformed glucose (Aiello and Key, 2002; Wrangham and Conklin-Brittain, 2003; Carmody and Wrangham, 2009; Wrangham, 2009). The increased energy yields are considered to be around 30% more than from similar quantities of foraged food (Carmody et al., 2016). Furthermore, cooking, even brief roasting, would have neutralized anti-nutrients such as plant secondary metabolites, and brought a wider range of starchy plants into the range of potential food sources (Carmody et al., 2011; Schnorr et al., 2016).

Cooking relies upon the control and manipulation of fire, the earliest evidence for which is widely debated. It has been argued that the control of fire and cooking developed around 1.8 million years ago when the larger brained *H. erectus* appeared in the fossil record (Wrangham et al., 1999; Aiello and Key, 2002; Leonard et al., 2003; Steudel-Numbers, 2006; Ungar et al., 2006a,b; Pontzer et al., 2011; Gao et al., 2017). Yet early evidence that distinguishes wild



**Figure 3.** Location of micromorphological sample in Klasies River Cave 1, MSA 1 phase. A) The carved block in the south-facing profile contains a thin layer of ashes overlain by a thicker layer of ashes and shell. B) Composite image of the two ash layers in thin section with arrows indicating relationships to the features in the field. Seven discrete units are visible here. From the base to the top: debris rich in bone and shell, ash, charred material and bone, ash mixed with shell, pure ash, debris rich in shell, sterile sand. PPL. C) Same view as (B) in cross polarised light (XPL). Botanical sample marked by red box in A. See SOM Figure S7 for detailed micrograph and analysis. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article). (Image and micrographs: S. Mentzer).



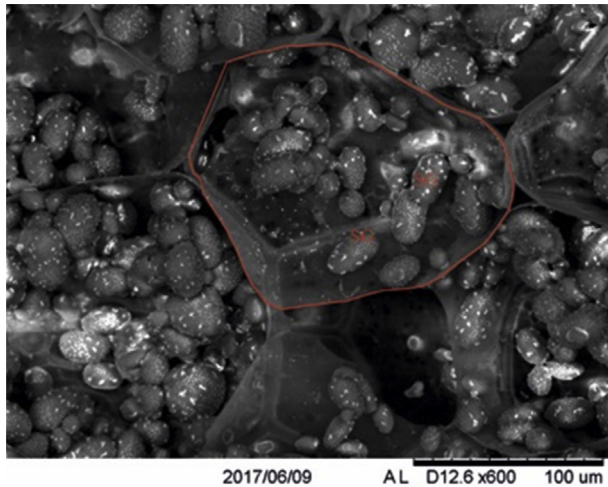
**Figure 4.** Location of the micromorphological sample in Klasies River Cave 1A, Howiesons Poort phase. A) The carved block in the north-facing profile contains a thick layer of ashes at its base (arrow). B) The block removed, with a thin dark layer (arrow) visible that divides the ash layer into two units. C) Composite image of the two ash layers in thin section, in plane polarised light (PPL). D) Same view as (C), in cross polarized light (XPL). The two ash layers are separated by a thin layer of debris that is visible here as an increased concentration of quartz sand (arrow). Botanical samples marked by red boxes in A. For the detailed micrograph and analysis see SOM Figure S7. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article). (Image and micrographs: S. Mentzer).

from anthropogenic fires is limited (Gowlett et al., 1981; Brain and Sillen, 1988; Bellomo, 1994; Chazan, 2017). Potential early evidence for cooking includes burned bones found at Wonderwerk Cave, South Africa, dated to 1 mya (Berna et al., 2012). Cooking is attested 800,000 years ago at Gesher Benot Ya'aqov (Alpersen-Afil, 2008; Alpersen-Afil and Goren-Inbar, 2010; Hardy et al., 2015; Melamed et al., 2016) by the discovery of charred plant and animal remains, in association with lithics. Repeated use of hearths at Qesem Cave, Israel, 300–400,000 years ago suggests a deep history of fire control, use and cooking (Shahack-Gross et al., 2014; Barkai et al., 2017).

The ability to make fire at will and thus to cook is evident at Klasies and may have been an enduring feature of human life at the site (Deacon and Wurz, 2005; Bentsen and Wurz, 2017; Wurz et al., 2018). The hearths that characterize Klasies River are small (c. 30 cm diameter) and were described by Deacon as lenticular in shape (Deacon, 2001; Deacon and Wurz, 2005). Experimental and ethnographic studies indicate that the overall shape and size of hearths can be related to the amount of fuel used and whether the hearth is cleared of ashes and debris between burnings (Mallol et al., 2007; Bentsen, 2013). Many of the Klasies hearths exhibit

layers of charred material overlain by white sediment that is consistent in appearance with ashes. Laterally extensive layers of blackened sediment and botanical remains were also documented at the site. Deacon and Geleijnse described these layers, as well as the basal charred portions of hearths as “carbonised partings” and whenever possible excavated them as discrete units (Deacon and Geleijnse, 1988: 7). After initial field identification, further study of these suspected hearths was warranted for two main reasons. First, some materials appear burned when they are not. For example, bones that appear charred might be stained (Shahack-Gross et al., 1997), humified wood can be mistaken for charcoal, and reddening of sediment can result from post-depositional moisture fluctuations (Stahlschmidt et al., 2015). Second, materials can be moved from the primary position of burning (the hearth) into secondary contexts by a variety of processes, including human site maintenance practices (Goldberg, 2003; Goldberg et al., 2009; Bentsen and Wurz, 2017) and it can be difficult to distinguish primary from secondary contexts using field observations alone. For this reason, micromorphology is invaluable.

Since 2013, micromorphological research and analyses of the stratigraphy and of putative hearths and other burned features



**Figure 5.** SEM micrograph from Klasies River modern reference collection: *Oxalis* sp. bulb with parenchyma (parenchyma cell outlined in red) filled with starch granules (marked as SG in red in photo). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article). (Micrograph: C. Larbey).

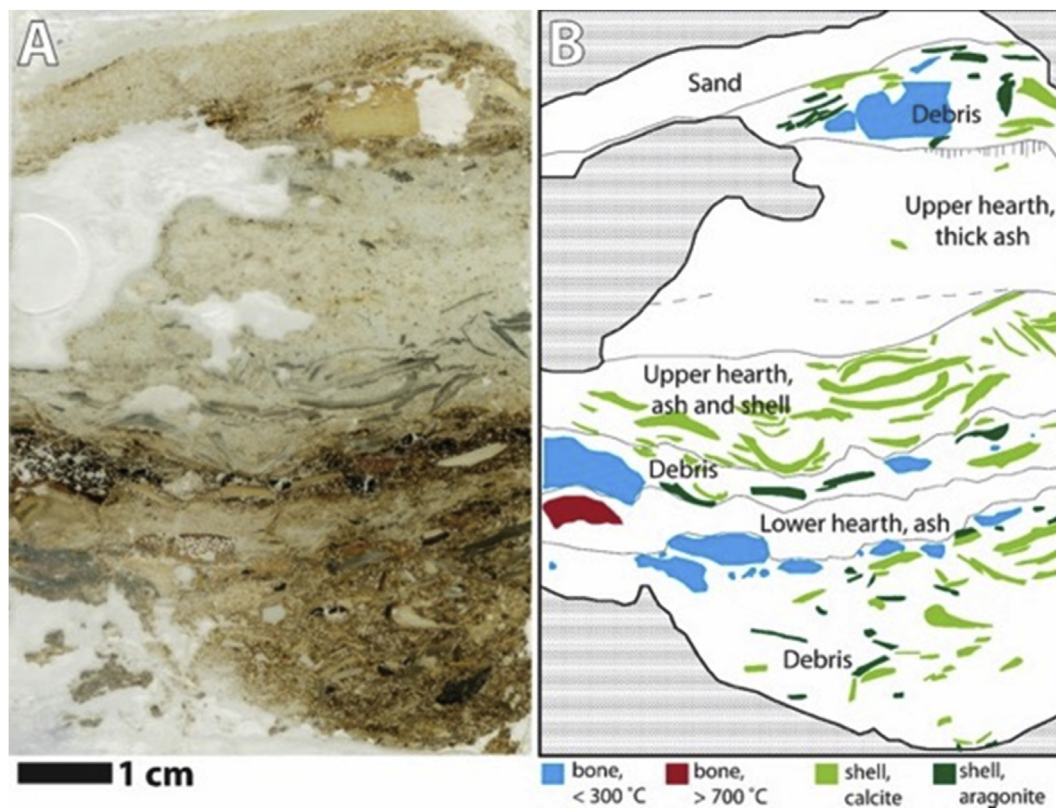
have been underway at Klasies River. Preliminary findings in 2015 had revealed a number of intact and undisturbed hearths in all areas of the site with identifications following criteria outlined in Mentzer (2012) and Mallol et al. (2017). Some key observations about these features include the fact that most hearths are

composed of a thin layer (ca. 1–2 mm) of charred organic material capped with a similar thin layer (ca. 2–4 mm) of ashes with variable preservation of the original calcite. The majority of these features are not lenticular in cross-section – a morphology that results from removal of fuel following burning (Mallol et al., 2007) – and furthermore do not exhibit multiple layers of fuel that might result from reuse. However, some hearths do exhibit these characteristics, and these are the most readily visible in the field owing to unusually thick ash layers.

As the current study aimed to recover and identify starch-bearing components of plants that: 1) had a high likelihood of being introduced to the site by humans, and 2) had been processed by cooking, the most favorable sampling localities were identified and readily visible hearths, and it was from these features in MSA1 and Howiesons Poort levels that samples were taken, alongside a few control samples away from hearths.

## 5. Methods

The methodology used a multi-disciplinary approach and a summary description of how the hearth contexts were identified and the sampling strategy for both hearth context and macrobotanical remains follows. Detailed descriptions of the methodology for the micromorphology, organic petrology, and micro-FTIR each can be found in the [Supplementary Online Material \(SOM\)](#). Laboratory analyses were conducted at the University of Cambridge (extraction and SEM imaging of plant remains) and University of Tuebingen (micromorphology, micro-FTIR, organic petrology).



**Figure 6.** FTIR measurements on the thin section from Cave 1, MSA 1 phase. A) Incident light scan of the thin section. B) Illustration of the important units, features, and results. The dashed line indicates the location of a possible surface within the upper ash layer that formed as a result of a short period of weathering between burning events. The vertical lines indicate a region of recrystallization. (Micrograph and Image: S. Mentzer)

### 5.1. Identifying hearths and hearth contents

If starch plant remains were to be identified as food, as opposed to bedding or incidental plant remains, the context for sampling was important. One of the key sampling strategies adopted here has been to remove botanical samples from intact hearths. It is difficult to identify intact hearths visually. The simplest forms of hearths are concentrations of burned materials that result from combustion of a fuel on top of an unprepared or minimally-prepared substrate. In the field, excavators identify suspected hearths by their roughly circular morphologies and composition, which often includes materials that are visually consistent with charcoal, ashes, and reddened sediment. In cross-section, i.e., the view in section profiles, these lenticular features can be identified by a tripartite stratigraphy consisting of a heat-altered substrate overlain by first a layer of charred material, and second, a layer of ashes (Meignen et al., 2002; Bentsen and Wurz, 2019); however, due to variability in substrate composition, conditions of combustion, and taphonomic processes, one or more of these layers may be absent (Mentzer, 2012).

In 2013, Dr. S. Mentzer and Prof. C. Miller, Tuebingen University, collected 27 sediment blocks intended for micromorphological analysis from profiles in Cave 1, Cave 1A and Cave 1B. Of these, 11 samples were considered to contain one or more hearths due to the presence of laterally discrete and thin lenses of wood ashes, or what appeared to be charred surfaces (carbonised partings), only some of which were associated with overlying layers of wood ashes. A further 12 blocks were collected in 2015, of which seven potentially contained hearths.

From these micromorphological analyses (Figs. 3 and 4), it was possible to identify the most promising localities to sample for botanical remains. A total of five botanical samples were collected. Four of the five samples were from contexts that were identified as containing multiple intact hearths. The remaining sample was a non-hearth sample from the Howiesons Poort level. The locations of the samples discussed in this paper can be seen in Figures 3 and 4.

In light of recent studies that challenge the common assumption that all materials recovered from within a hearth are contemporaneous with the burning event, it is especially important to understand the stratigraphic associations between burned materials (Mallol et al., 2013b). In the case of the hearths sampled for botanical remains, the hearths solely comprised layers of ash from which the botanical remains were recovered. These hearths were set on layers of anthropogenic debris, not contemporary with the hearth.

A number of common approaches to the identification of heated materials in primary position were used and are summarized in Bellomo (1994), Mentzer (2016), and Weiner (2010).

One additional aim of applying multiple types of analyses to different components of a single micromorphological sample is to identify discrete depositional events, or microscopic contexts (Goldberg et al., 2017). All but one of the botanical samples that yielded fragments of parenchyma were taken from immediately next to the micromorphology scars (see Figs. 3 and 5) in order to facilitate integration of all observations.

Organic petrology reflectance measurements were taken to a) distinguish humified from charred material; b) reconstruct the conditions of humification (Jacob, 1974, 1980; Schwaar et al., 1990; Borrego et al., 2006); c) reconstruct the conditions of charring (Jones et al., 1991; Guo and Bustin, 1998; Bustin and Guo, 1999); d) identify other materials such as fat-derived char (Ligouis, 2017); and e) observe other plant tissue morphologies and features that are characteristic of tissue type or taphonomic processes. These types of analyses have been applied previously to document conditions of combustion for burned materials in South African Middle Stone Age contexts (Goldberg et al., 2009).

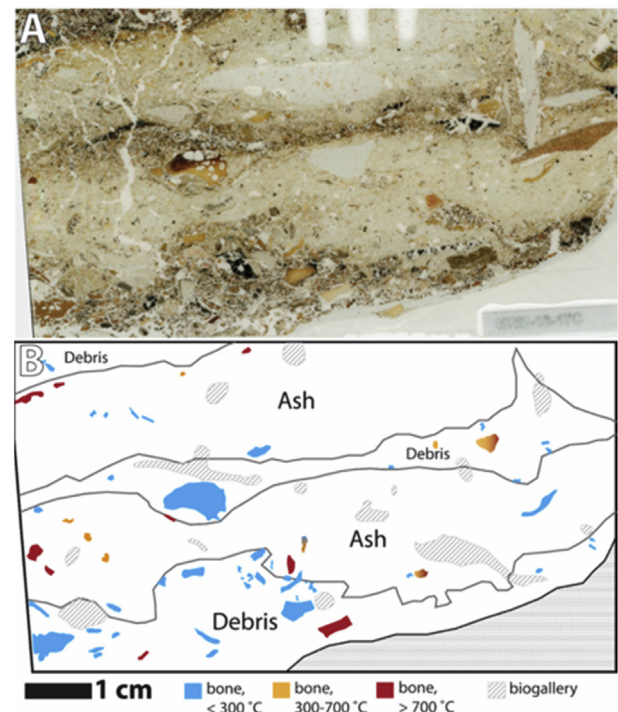
The relationships between the micromorphology samples, botanical samples, and the sampled excavation profiles are shown in Figures 3 and 4. The micromorphology thin section corresponding to the sample location within the witness baulk of Cave 1 contains two discrete hearths sandwiched between layers of sand mixed with anthropogenic debris. The macroscopic fragments of parenchyma tissue were recovered from the upper of the two hearths. The thin section corresponding to the sample location in Cave 1A also contains two discrete hearths.

**Sample 5, MSA 1 phase, Cave 1** The MSA 1 levels in Cave 1, ~120 kya, represent the oldest at Klasies River. Evidence of occupation starts just above the bedrock. The ash layer 25 cm above bedrock, representing an intact hearth, was sampled. Sample 5 was removed from the south section, of the Witness Baulk (see Figs. 2 and 3). This face was exposed by Singer and Wymer in 1967 and 1968 and the sample corresponds with Level 38 from those excavations in Cave 1 (Singer and Wymer, 1982).

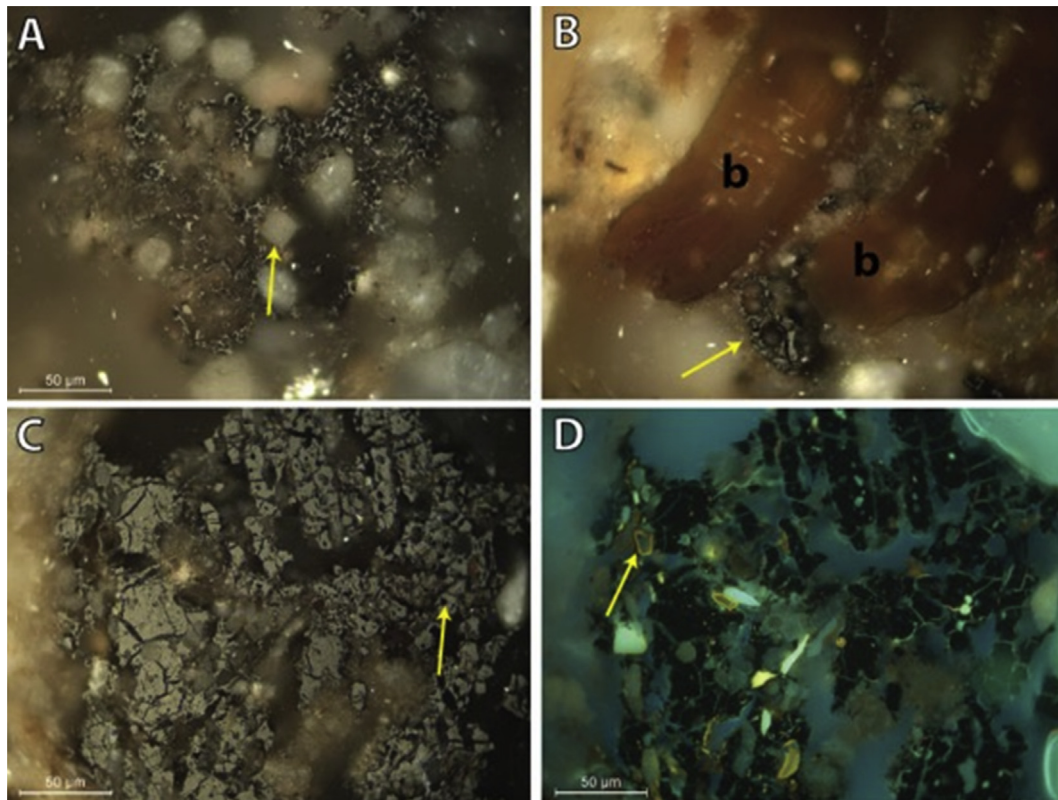
**Samples 1 and 3, Howiesons Poort phase, Cave 1A – Top Cutting** Samples 1 and 3 were taken from the south-east face, F50. This section was exposed by Singer and Wymer's excavations in 1967/68 and the samples come from levels 15–17 from that excavation (Singer and Wymer, 1982). This section is associated with the Howiesons Poort techno-complex (Wurz, 2008) occurring within the upper 1.5 m of the sequence. The intact hearth is located in a context dated to ca. 65 kya (Vogel, 2001; Jacobs and Roberts, 2017). The botanical sample included non-hearth sediments as well as ash but the ash layers were separated with a knife and dental tools from the other sediment layers (Fig. 4).

### 5.2. Macro-botanical sampling and analysis

Experiments had shown that charred fragments disintegrated in water because of the presence of solutes in the charred fragments;



**Figure 7.** FTIR measurements on the thin section from Cave 1A, Howiesons Poort phase. A) Incident light scan of the thin section. B) Illustration of the important units, features, and results (Biogallery = the burrows made by animals through the stratigraphy). (Micrograph and image: S. Mentzer).



**Figure 8.** Klasies River, MSA 1 levels, Cave 1 - organic tissues and substances from the upper hearth under reflected and UV light. A) Poorly preserved plant tissue associated with wood ashes (arrow). This level of decomposition prevents further measurements or identification. B) Two corroded bone fragments (b), one of which is associated with fat-derived char (arrow). The fissures within the char are indicative of degradation. C) A complex plant tissue with reflectance of 0.6%Ro. Holes visible on the right side of the image (arrow) indicate fungal attack of the wood prior to burning. D) Same view as (C), UV light. Multiple phases of permineralization are visible. Greenish zones indicate infilling of pores by carbonate, while yellow zones indicate phosphate. In some cases (e.g., arrow), phosphate-filled pores later filled by carbonate. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article). (Micrographs: B. Ligouis).

therefore flotation was not the ideal sampling strategy for these caves (Larbey, 2019). Also the standard method for recovery of botanical samples is using sediment that has already been excavated, i.e., where sediment has already been raked over with a trowel. The process of trowelling can destroy fragile charred fragments. To avoid these circumstances, block botanical samples were carved from next to micromorphology scars, using knives and leaf trowels.

Only two of the paired micromorphological and micro-excavated botanical samples are discussed in this paper. One pair from Cave 1 MSA 1 deposits (Sample 5) and one pair from Cave 1A Howiesons Poort deposits (Samples 1 and 3).

The samples were micro-excavated at the George Pitt Rivers Laboratory in the McDonald Institute for Archaeological Research, University of Cambridge. This process included an initial screening under a stereo-microscope (Nikon SMZ800  $\times 10$ ,  $\times 20$  and  $\times 40$  magnification), using featherweight spring forceps and dental tools looking for burned parenchyma fragments. Microstratigraphic units were excavated individually and the context of possible parenchyma fragments was noted. Putative plant remains were then mounted onto scanning electron microscope (SEM) stubs, using carbon tabs; each stub was mounted on a pin and analyzed through an environmental Hitachi TM3000 SEM. The SEM analyses were made on full vacuum, in ‘Analyze’ mode. The magnifications were  $\times 30$  and  $\times 40$  for whole fragment images and  $\times 300 - \times 500$  for parenchyma and feature images. No gold sputter coating was used for these samples so that samples are available for future analysis.

For each fragment, a whole image micrograph was taken and then subsequent images as appropriate. The archaeological fragments are curated and stored on the SEM stubs in labelled stub boxes in the George Pitt Rivers Laboratory.

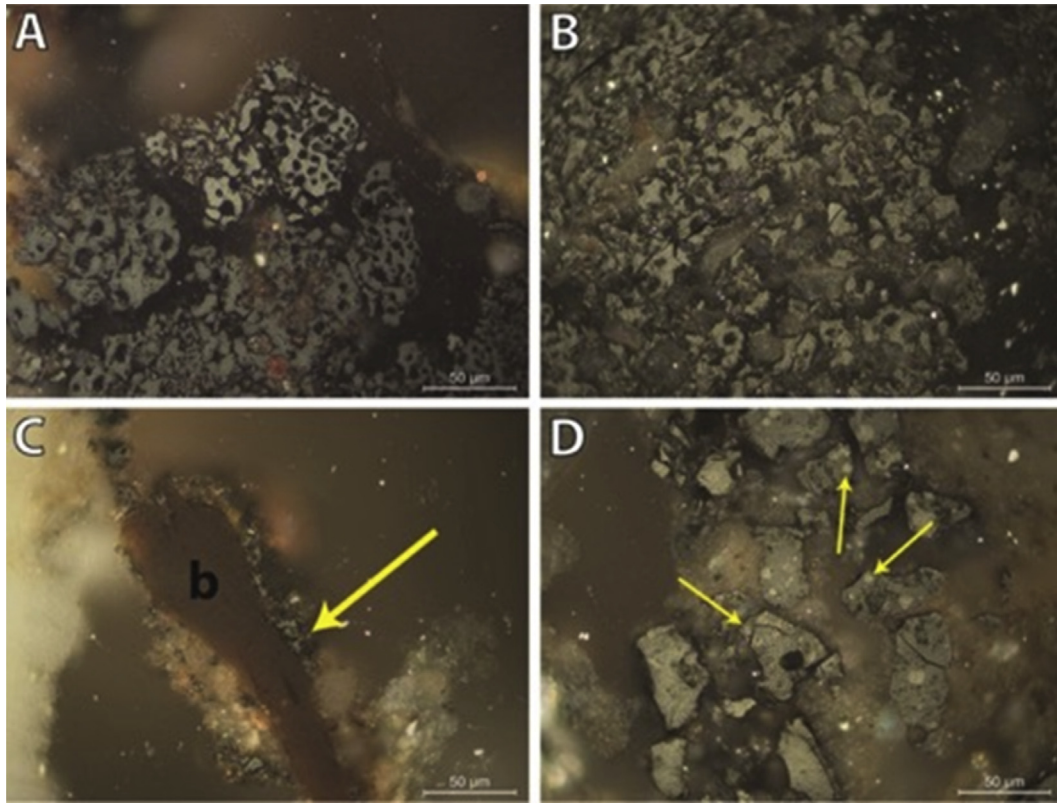
### 5.3. Parenchyma identification and analysis

Parenchyma is a relatively undifferentiated tissue that contains the starch granules, the energy source, stored by green plants and used for future growth (Pérez et al., 2009; Preiss, 2009) (Fig. 5).

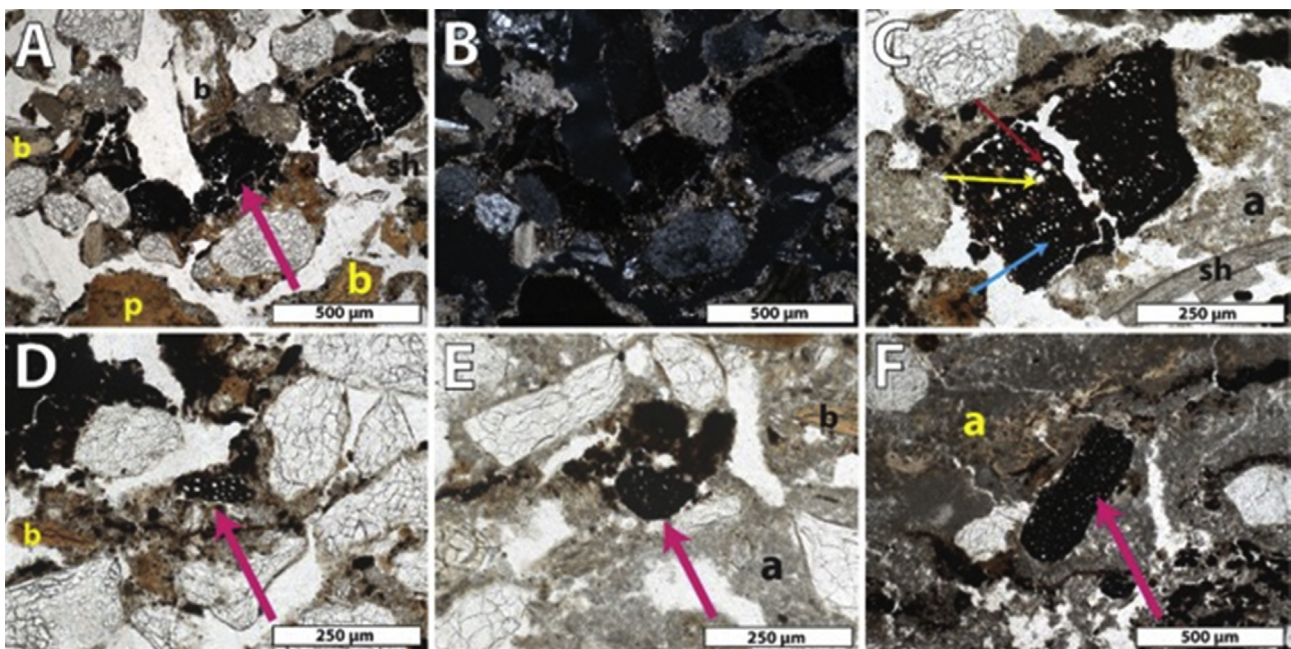
Identification of parenchyma was made by comparison with reference texts and methods mostly described by Hather (1988, 1993, 2000) and by comparisons with the modern reference collection taken from around Klasies River.

Despite the undifferentiated nature of parenchyma derived from underground storage organs, there are features such as the organisation of vascular bundles (the means of distributing food and water to the storage organ) that will determine if the plant was a monocot or dicot. Terminal buds (the distal end of the tuber), and detachment scars (where the tuber has been attached to the plant) will distinguish tubers from bulbs (Hather, 1993, 2000). Features such as secretory cavities (where the plant secretes substances, such as secondary metabolites, to repel phytophagous animals), and latex ducts (which are often near the surface and offer the plant's underground storage organ protection in the case of wild fire), help in the identification of starchy plants (Hather, 2000).





**Figure 9.** Klasies River, Howiesons Poort phase, Cave 1A - organic tissues and substances under reflected light. A) Plant tissue with visible structure, and variable reflectance. B) Poorly-preserved plant tissue with localized carbonate precipitation within the structures. C) Fragment of heated bone (b) coated in fat-derived char (arrow). D) A concentration of char with inclusions of oil, evidenced by Newton rings (arrows). (Micrographs: B. Ligouis).



**Figure 10.** Parenchyma visible in thin section. A) A fragment of rhizome parenchyma from Klasies River, Howiesons Poort phase, Cave 1A (arrow), PPL. Fragments of bone (b) and a phosphatic grain that may be guano (p) are also visible. B) Same view as (A), XPL. C) Detail of the fragment with identifiable structures related to a vascular bundle in the stele of the rhizome, PPL. Blue arrow: parenchyma. Yellow arrow: xylem. Red arrow: phloem. Also visible: shell (sh) and ash (a). D) Another fragment of unidentified parenchyma from Cave 1A (arrow), PPL. E) Unidentified parenchyma fragment from Cave 1A (arrow), PPL. F) Unidentified parenchyma fragment from MSA 1 phase Cave 1 (arrow). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article). (Micrographs: S. Mentzer)

**Table 1**  
Summary of botanical results from all three samples. Unid = unidentified.

Sample 5		Sample 1		Sample 3	
No. Fragments	Category	No. Fragments	Category	No. Fragments	Category
Ashy Layer		Ash Layer		4	Parenchyma
4	Rhizome parenchyma	12	Monocot parenchyma	2	Aerenchyma
2	Tuber parenchyma	5	Monocot tissue	7	Fused starch
4	Monocot parenchyma	5	Parenchyma	18	Unid plant xylem
5	Parenchyma	1	Fused Starch & druse crystal	4	Wood charcoal
6	Wood charcoal	3	Wood charcoal	35	Total
5	UNID plant xylem	26	Total Ash Layer		
26	Total Ash Layer	Carbon-rich Substrate			
Carbon-rich Substrate		9	Wood (charcoal)		
8	Fused starch fragments	4	Secondary root xylem		
5	Monocot vascular tissue	18	UNID Plant xylem		
2	Plant tissue with raphides	31	Total Substrate		
2	Seed testa				
35	Wood charcoal				
42	UNID plant xylem				
94	Total Substrate				

## 6. Results

### 6.1. Identifying hearths and hearth contents: results of micromorphology and FTIR analyses

Some results of the micromorphological analyses of the two sampling contexts are presented in [Figures 3 and 4](#) (see also SOM). Both contexts contained multiple layers of debris mixed with charred material overlain by layers of wood ash.

Micro-Fourier-transform infrared spectroscopy (Micro-FTIR) analyses were conducted on fragments of bone from the micromorphology thin sections, located within and beneath the ash layers, in order to estimate heating temperature ranges (see SOM for classification criteria). Similar work has been conducted in other Palaeolithic and Stone Age contexts by Berna and colleagues ([Berna and Goldberg, 2007](#); [Dibble et al., 2009](#); [Berna et al., 2012](#); [Goldberg et al., 2012](#)). Analyses were also conducted on fragments of shell in ash and debris layers in the FTIR sample from MSA 1 phase in Cave 1. Marine shells, depending on species and environmental conditions, may be composed of aragonite, calcite, or a combination of the two calcium carbonate polymorphs. When heated to ~550 °C or higher and then cooled, the majority of the aragonite breaks down and recrystallizes to calcite ([Toffolo and Boaretto, 2014](#)). The mineralogical composition of the shell fragments was measured in order to provide further information about heating temperatures within the ash layers and substrates.

The locations of micro-FTIR measurements on bone and shell and results of the temperature classifications are illustrated in [Figure 6](#) (paired with Sample 5, MSA 1) and [Figure 7](#) (paired with Samples 1 and 3, Howiesons Poort). In the sample paired with Sample 5, MSA 1 ([Fig. 6](#)), the results indicate that the majority of the bone fragments observed in thin section are both associated with the debris layers and have been either burned at low temperatures

or have not been exposed to any heat. The single large bone fragment embedded in the lower hearth was heated at or above 700 °C. The results of the mineralogical analyses of the shell fragments are also illustrated in [Figure 6](#). Debris layers contain shell fragments composed of both calcite and aragonite. In contrast, the ash layer containing abundant shell fragments contains only shells composed of calcite. In addition, shell fragments located within the ash layer and the debris layers that exhibit petrographic characteristics consistent with burning ([Villagran et al., 2011](#)) are all composed of calcite.

These results strongly suggest that temperatures within the ash layer exceeded 550 °C. The presence of aragonite shells within the upper portions of the debris layers further suggest that indirect heating of the hearth substrate never exceeded 550 °C or only reached high temperatures for a short duration of time. These findings are consistent with experimental measurements of hearth substrate temperatures, which vary according to length and intensity of burning, substrate composition, moisture and shielding effects of ash ([Aldeias et al., 2016](#)).

In the Howiesons Poort (HP) deposits, more bone fragments show evidence of heating, with three fragments exhibiting heating gradients. Thirteen of the 17 bone fragments heated at moderate to high temperatures are associated with the ash layers.

### 6.2. Identifying hearths and hearth contents: results of organic petrology analyses

Some results from the organic petrology samples from Cave 1 and 1A are illustrated in [Figures 8 and 9](#). The sample from Cave 1, MSA 1, indicates that preservation of the majority of the plant tissues was poor, which prevented both morphological identifications of a majority of the fragments and collection of reflectance measurements. Both the lower and upper debris layers contained a

**Table 2**  
Summary of archaeological macro-botanical plant remains from Klasies River featured in text.

Sample location	Fragment No.	Identification	Key features	Dimensions mm (max)
MSA 1	1	Parenchyma	Vascular bundle and intercellular piercing	6.7 × 5.8
	2	Parenchyma	Vascular bundles	4.4 × 2.8
	3	Rhizome parenchyma	Disrupted cell matrix indicating cooked from fresh	1.7 × 1.7
	4	Raphides		
Howiesons Poort	5	Monocot parenchyma	Monocot vascular bundles	3.8 × 2.3
	6	Rhizome parenchyma	Disrupted cell matrix indicating cooked from fresh	1.6 × 1.6
	7	Parenchyma	Cortex and relict vascular bundle	2.6 × 1.6
	8	Aerenchyma	Isodiametric parenchyma chains	1.1 × 1.2
	9	Druse Crystal	Druse crystal in fused starch	2 × 1.9

mixture of woody and herbaceous plant tissues. In contrast, a wider variety of tissue types was identified in the sample from Cave 1A, Howiesons Poort: stems, leaves, fibrous tissues and woody tissues. Much of the poor preservation of the plant tissues in Cave 1 is due to extensive permineralization, including formation of phosphate minerals and secondary carbonate. Plant tissue from Cave 1A was also either poorly preserved or partially/entirely mineralised. The poor preservation of some of the plant tissue may have been caused by humification and fungal attack prior to burning. In both sampling localities there were differences between individual hearth layers in the type and extent of permineralization and also fragmentation of plant tissues, which indicates that the dominant post-depositional processes varied between burning events.

In the sample from Cave 1 where reflectivity measurements were possible, the moderately low values (0.6–0.7%Ro) indicate burning temperatures of around 150–200 °C. These values are typical of fuel from fires that are allowed to burn to completion. Fat-derived char was observed in association with a few bone fragments, although the preservation of this material was poor. In the sample from Cave 1A, the distribution reflectance values indicate that a majority of fragments are humified, but burned tissues are also present. Fat-derived char is also present as isolated particles and also associated with bone (see Fig. 9D), the latter indicating that the bones were heated while fresh.

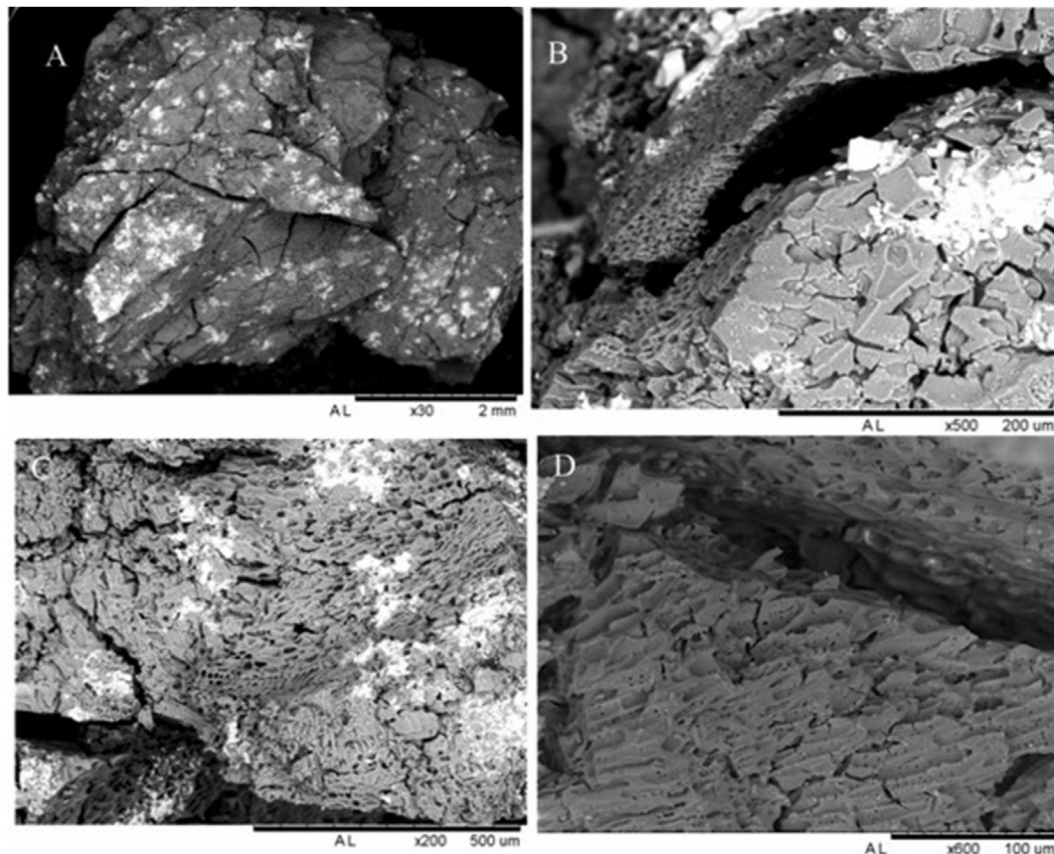
### 6.3. Identifying hearths and hearth contexts: synthesis

A full synthesis of the micromorphology with other micro-contextual analyses is provided in the SOM. Both sample localities are notable for having evidence for multiple hearths that were

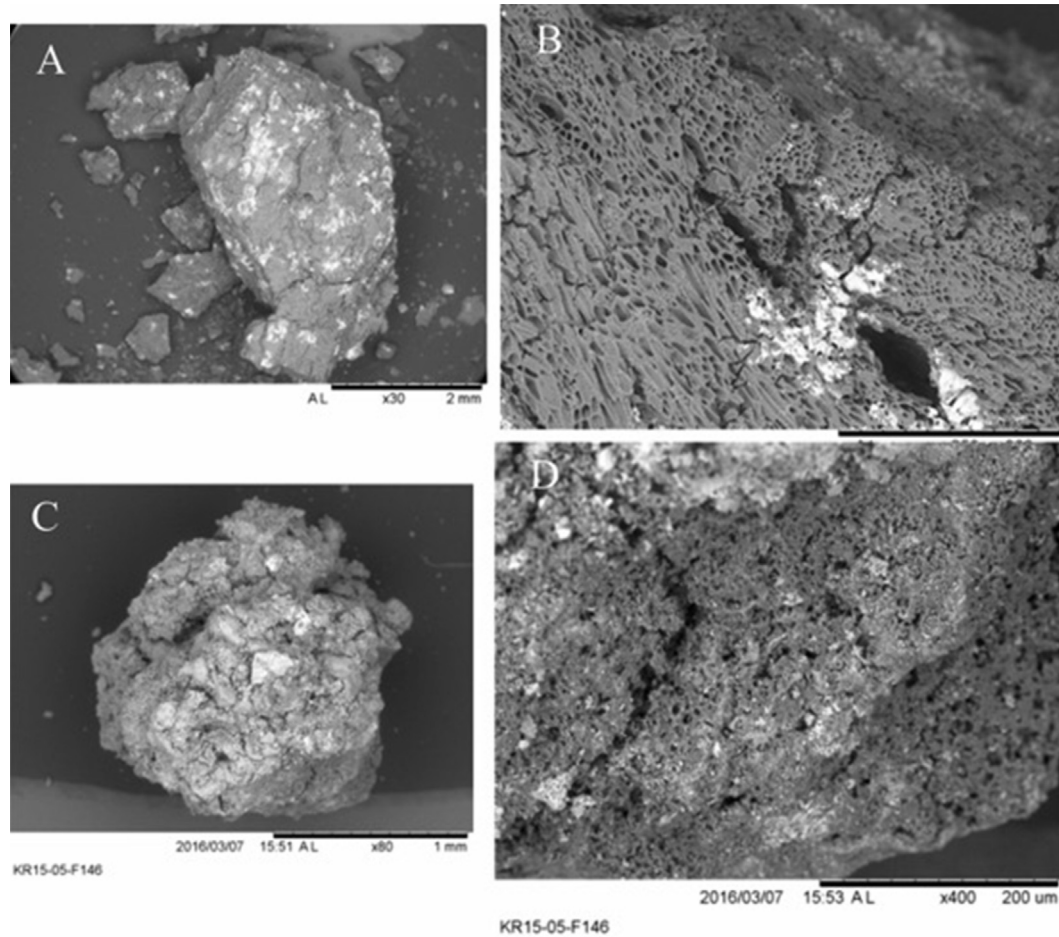
constructed in the same location. All three types of analyses support the interpretation that the sampled ash layers are associated with intact hearth features containing heated anthropogenic materials. In Cave 1, the upper hearth that yielded fragments of parenchyma tissue contains at least two, and possibly more, discrete layers of ashes that represent multiple burning events in close succession (see Fig. 3B). Two possible layers of ash separated by a thin recrystallized surface are also present in the upper of the two hearths from the Howiesons Poort phase. These types of internal stratigraphy, observed in other Pleistocene contexts (Berna and Goldberg, 2007; Wadley et al., 2011; Mallol et al., 2013a; Shahack-Gross et al., 2014) are suggestive of reuse of an active hearth structure for repeated burning events, perhaps with very short intervals (on the scale of days) of surface exposure in between. The variable heating of materials within the debris layers, the upper surfaces of which comprise the charred hearth bases (c.f. Mallol et al., 2013b), indicates that the carbonised partings in the sampling localities are best interpreted as burned surfaces with additions of hearth fuel remnants. Notably, the parenchyma tissues described above derived not from the hearth bases, but from the overlying ash, and thus the association with the firing (cooking?) event is secure.

### 6.4. Macro-botanical results

Plant remains including parenchyma were recovered from the hearth-related samples: Fragments of parenchyma were identified in thin sections from both sample localities. Figure 10 illustrates the parenchyma fragments from both Cave 1 and Cave 1A. Given the limitations of the random cross-sections through the tissues, it is



**Figure 11.** SEM micrographs of parenchyma fragments from hearth in MSA 1 phase, Cave 1, Klasies River: A) whole image of fragment 1 (B) shows parenchymous tissue (C) and (D) show transverse longitudinal section (TLS) view of vascular structure and intercellular pits in parenchyma cells (SEM micrographs lightened) (Micrographs: C. Larbey).



**Figure 12.** SEM micrographs of parenchyma fragments from Klasies River, Cave 1 MSA 1 phase: Fragment 2 - (A) whole image (B) shows vascular bundles in the parenchyma; Fragment 3 - (C) whole image (D) showing rhizome pith parenchyma (SEM micrographs lightened) (Micrographs: C. Larbey).

impossible to make further identifications in most cases as to plant type. Nevertheless, fragments of parenchyma were documented in all four hearths recognized in thin section.

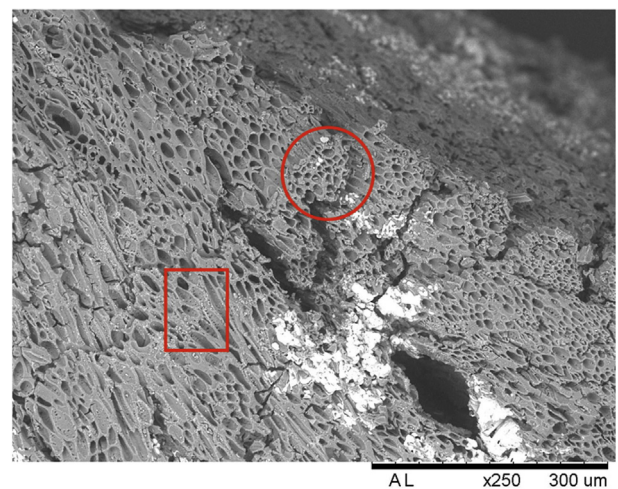
The macro-botanical analysis results from all samples included wood charcoal and the parenchymous remains of rhizomes and tubers. In both hearths, the plant remains came from the ashy levels of the hearths, rather than any charred-looking layers. The contexts and locations of the botanical samples can be seen in more detail in the SOM: MSA 1 at [S2](#), [S3](#) and [S4](#) and Howiesons Poort at [S5](#), [S6](#) and [S7](#).

The results from these three samples can be seen in [Table 1](#).

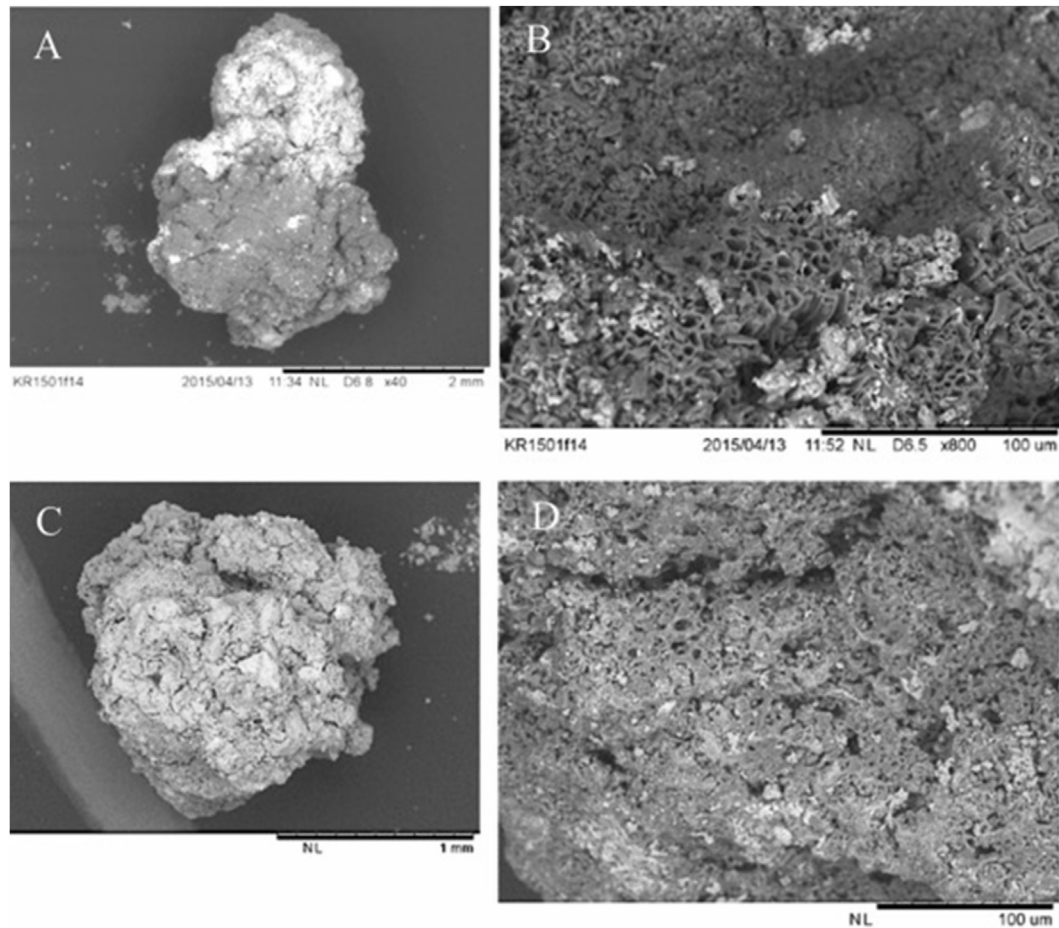
The earliest plant remains come from a hearth situated 25 cm above bedrock in Cave 1 in the phase equating to MSA 1, broadly equivalent to MIS 5e (~120 kya). The later Howiesons Poort phase samples come from a hearth around the middle of the Howiesons Poort sequence in Cave 1A. Parenchyma fragments and features indicating potential starchy plants are summarized in [Table 2](#).

It is often difficult to determine from which part of the root or tuber the fragment comes, mainly because there are either no features or the orientation is difficult. In the case of the fragments from Klasies River, very few features remained that would allow either identification or orientation to the parent root or tuber. The identifications made derived from the distinctive arrangement of vascular bundles that are characteristic of monocot rhizomes. In the case of rhizomes, the pith parenchyma that runs down the middle of the rhizomes, was used for identification, rather than, as with a tuber, the parenchyma that is found throughout the storage organ ([Hather, 2000](#)).

The fragment in [Figure 11](#) shows parenchymous tissue (B) parenchyma surrounding vascular bundles (C), and parenchyma cells with intercellular pits visible (D). There are no features to indicate the type of the underground storage organ.



**Figure 13.** SEM micrographs of parenchyma fragments from a hearth in MSA 1 phase, Cave 1, Klasies River: Fragment 2 (see also [Fig. 11](#) A and B). Oblique transverse section (TS) view of monocot rhizome vascular bundles (in circle) and parenchyma lumina in box (Micrograph: C. Larbey).



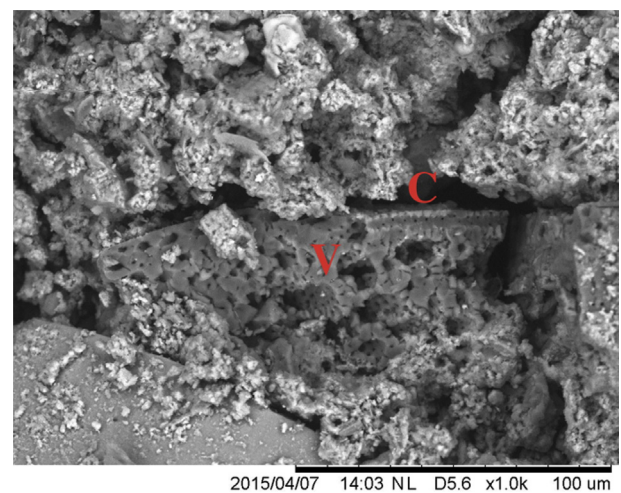
**Figure 14.** SEM micrographs of parenchyma fragments from a hearth in Howiesons Poort phase, Sample 1, Cave 1A, Klasies River: Fragment 5 (A) whole image (B) vascular bundles and rounded cells of monocot parenchyma. SEM images of Fragment 6 (C) whole image (D) rhizome parenchyma identified from criteria described by Hather (2000) (SEM micrographs lightened) (Micrographs: C. Larbey).

The vascular structure of fragment 2 in Figure 12 A and B is distributed across the rhizome in bundles, similar to the distribution that is found in monocotyledonous flowering plants. Many monocots have starchy tissue bodies and monocot plant structures have been observed in the charred fragments throughout these hearths, sometimes but not always associated with parenchyma. The SEM micrograph images of fragment 3 at in Figure 12C and D show rhizome pith parenchyma, exhibiting a characteristic distortion of the vesicular matrix. This distortion indicates that the rhizome was probably charred while fresh. According to Hather this distortion results from the expansion of moisture during heating and escape of steam (Hather, 1993). One of the key purposes of underground storage organs is to store water underground (the definition of geophytism) (Proches et al., 2006). The water content of most roots and tubers is high, i.e., 45%–81% in Asteraceae roots and tubers (Tertuliano and Figueiredo-Ribeiro, 1993) and 77%–89% in Liliaceae bulbs (Incoll et al., 1989). The high water content that would have characterized the fresh rhizome in Figure 12D would indicate that it was not a suitable source of fuel, and so it was more likely cooked as food.

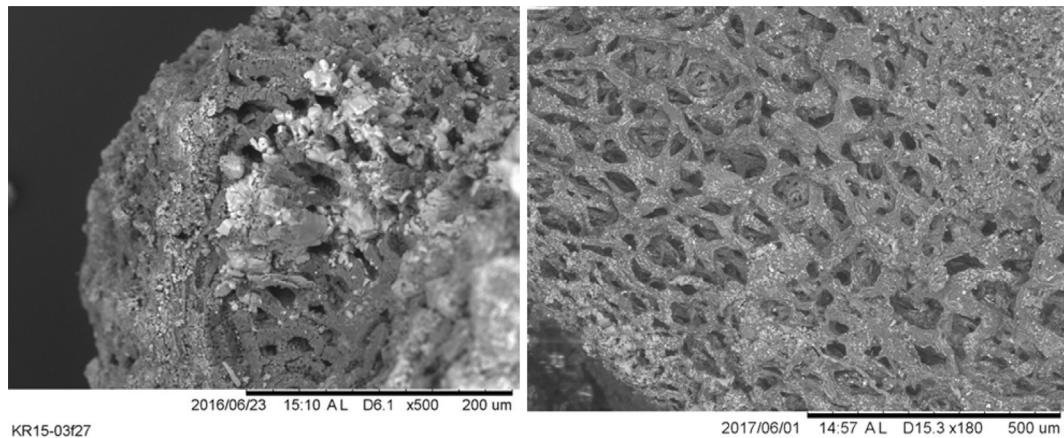
The regular grouping of vascular bundles seen in Figure 13 suggest a monocot underground stem tuber. Monocots form the major part of all underground storage organ species and are common around Klasies River.

The fragments illustrated in Figure 14 came from Cave 1A and date to ca. 65 kya. The parenchyma fragments were recovered

during careful micro-excavations of the samples, with these fragments coming only from within the ashy layers of the hearth immediately above a charred substrate. The substrate comprised heavily fragmented, charred, non-vascular plant tissue.



**Figure 15.** SEM micrograph from Howiesons Poort phase, Cave 1A, Klasies River: Fragment 7 shows parenchyma and collenchyma under cortex (under C) and relict vascular bundle as in the semi-circular tube shape under V. (Micrograph: C. Larbey).



**Figure 16.** Fragment 8, Sample 3, Cave 1A (Left) archaeological aerenchyma exhibiting isodiametric chains of parenchyma cells (Right) aerenchyma from *Nymphaea nauchauli*, the only water lily species indigenous to South Africa and part of the modern reference parenchyma collection (Micrographs: C. Larbey).

Parenchyma is visible in Figure 14B, along with vascular bundles typical of monocot stem parenchyma (Hather, 1993). Rhizome pith parenchyma is visible where the tissue has deteriorated in a vesicular matrix (Fig. 14D), again indicating this is more likely to be a food remnant than fuel.

Parenchyma visible under the cortex, with a distinct line of collenchyma cells, and relict vascular bundles can just be seen (Fig. 15).

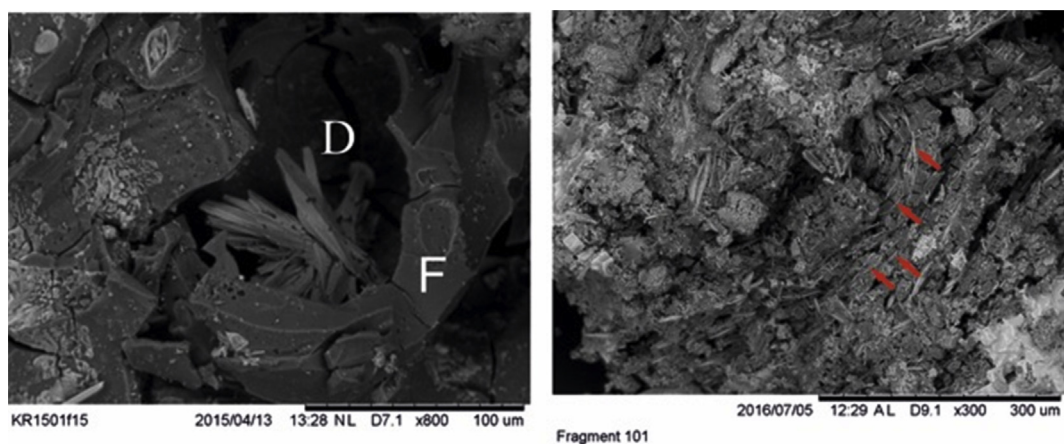
Aerenchyma is another form of parenchyma found in aquatic and semi-aquatic plants. The parenchyma cells are organized in isodiametric chains that create or surround air spaces, providing the rhizome or tuber of plant species such as water lilies (Nymphaeaceae) or reeds and rushes (*Typha* sp. or *Juncus* sp.) with both oxygen and buoyancy (Hather, 2000). A fragment of aerenchyma was recovered from Sample 3, Cave 1A, Howiesons Poort level. This fragment of aerenchyma exhibits isodiametric parenchyma chains under the cortex, indicating an aquatic species of rhizome or tuber (Fig. 16). For comparison, the water lily tuber (*Nymphaea nauchauli*) from the modern reference parenchyma collection shows aerenchyma under the cortex, as with the archaeological fragment. The presence of this fragment strongly suggests that starchy plants were also being exploited from fresh water resources.

If parenchymous tissue is not visible, the presence of starchy plant tissue can sometimes be inferred by the presence of calcium oxalate crystals. In the case of the Klasies River samples, a druse crystal, contained within fused starch (Fig. 17) suggests the presence of starchy plants. Druse crystals are rare in parenchyma and occur most often in Liliaceae and Iridaceae species (Hather, 2000), both of which are abundant in the Cape Floristic Region and around the Klasies River site.

Raphide and druse crystals have been observed in the archaeological assemblage and modern reference collection. One of the functions of the crystals is as a defensive mechanism against herbivory; they are formed of calcium oxalates or occasionally of calcium carbonates. These crystals occur throughout both the archaeological and modern reference assemblages and can be diagnostic. The raphide crystals (Fig. 17) are common to Liliaceae and Iridaceae families. It appears that cooking does not entirely break down the crystals (Hather, 2000).

## 7. Discussion

The Klasies River hearths sampled for this research are consistent with those that characterize the site, described by Deacon and colleagues as small (c. 30 cm diameter), circular ash-filled



**Figure 17.** Archaeological fragments containing calcium oxalate crystals from Klasies River Howiesons Poort phase (Left) Fragment 9, exhibits a druse crystal (D) within a remnant idioblastic cell surrounded by fused starch (F) (Hather, 2000) (Right) Fragment 4, sample 5, MSA 1, raphide crystals are indicated by red arrows (Micrograph: C. Larbey). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

depressions (Deacon, 2001; Deacon and Wurz, 2005). Deacon suggested that these were domestic hearths that contained burnt food remains and each may have belonged to a nuclear family unit (Deacon, 1993, 1995). The association of small hearths with starch plant remains and domestic food preparation has also been inferred from carbonised matter at Strathalan Cave in the Drakensberg foothills, South Africa (Opperman, 1996) and we note the similarities.

Klasies River, as part of the Greater Cape Floristic Region, comprised a mosaic of subtropical thicket, coastal dune thicket, South Coastal Afrotropical forest, and littoral vegetation, with fynbos elements (Parkington et al., 2000; Proches et al., 2006; Cowling et al., 2009; Quick et al., 2016; Singels et al., 2016; van Wijk et al., 2017). This ecosystem is rich in roots and tubers that would have provided a year-round consistent source of energy (Bergh et al., 2014). These resources also appear to have included fresh water roots and tubers, evidenced by the presence of aerenchyma in this assemblage. While semi-aquatic sedge grasses have been used for bedding at Sibudu, there is no evidence for this practice at Klasies River, suggesting that these fresh water tubers were being used as food. The ability to remember ideal foraging times for particular plant species, to distinguish edible plants from poisonous species, to identify those that are not poisonous at certain times of year or need to be cooked before being eaten or those that have sweet bulbs in the spring but are woody in the autumn and to memorize the location of tubers that contain large amounts of water require an 'ecological intelligence' (Jones, 2009: 173). Monocot plants quite frequently have starchy underground storage organs. Jones also points out that this 'intelligence' could be used to identify monocot plants that frequently have USOs. Monocots have a number of distinctive features such as long parallel veins on the leaf that act as an above ground flag. Humans, like great apes, have discovered that if they follow this leaf back to the stem base, then there is a high probability there will be some accessible high energy, toxin-free food to be found, such as a bulb or a rhizome (Jones, 2009: 174). Monocot species were a common feature of the parenchyma assemblages from Klasies River. This is not surprising as there are more than 2000 species of geophytes in the Cape Region, 83% of which are monocots (Proches et al., 2006). Among the species of monocots found around Klasies River are species of *Watsonia* (Iridaceae), *Hypoxis* (Hypoxidaceae), *Oxalis* (Oxalidaceae), *Chasmanthe aethiopica* (Iridaceae), *Spiloxene* (Iridaceae), *Haemanthus albiflos* (Amarillidaceae), *Ornithogalum graminifolium* (Hyacinthaceae or Scilloideae), *Trachyandra ciliata* (Asphodeloideae) and *Cyperus usitatus* (Cyperaceae). Many of these families belong to the Asparagales order, which correlates with the prominence of Asparagales among current Cape geophytes orders. Of the 1463 endemic Cape geophyte-bearing monocot species, 1156 (79%) are found in the Asparagales order (Proches et al., 2006). Dried corm scales, leaf sheaths and tubers of *Watsonia*, *Hypoxis* and *Cyperus* have been found in Later Stone Age (LSA) caves and shelters across South Africa, including Melkhoutboom Cave, Scott's Cave and Strathalan B Cave, Rooikrans Cave, Sehonghong Rockshelter, Collingham Shelter, Highlands Cave and HaMakatoko Shelter (Deacon, 1976, 1993; Opperman and Heydenrych, 1990; Nic Eoin, 2016; van Wijk et al., 2017). Studies of early Khoisan also recorded exploitation of these taxa (Lichtenstein, 1847; Steyn, 1990).

The importance of the role of starchy plant foods in human evolution is only just beginning to be fully understood. The genetic and biological evidence strongly suggests that there were powerful selective pressures for a diet that contained a significant element of starchy carbohydrates (Lazaridis et al., 2014; Hardy et al., 2015; Inchley et al., 2016). Research within the Cape region found that, while marine resources might be seasonally limited by storms and

tides and terrestrial resources impacted by high rainfall and periods of high aridity, roots and tubers provided a reliable year-round food source (Singels et al., 2016). Fallback foods, however, cannot be responsible for one of the largest selective sweeps in the human genome. The significance of the early human starch diet must have come from the benefits of a reliable energy source.

The presence of parenchyma in hearths, although not identified to species, together with heated shell and heated bone would suggest that multiple foods were being cooked. We can infer that the early human hunter-gatherers of Klasies River were consuming cooked starchy plants as early as ~120 kya in MIS 5e, which continued during MIS 4.

## 8. Conclusion

These findings from Klasies River provide direct evidence that AMH, in addition to the rich coastal resources for which there is abundant evidence, were consuming cooked plant starches. An early human diet rich in starchy plants resonates with human genetic evidence indicating that plant starch is not a recent component of the modern human diet, but has an antiquity comparable at least to that of *H. sapiens* itself.

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## Declarations of interest

None

## Supplementary Online Material

Supplementary online material to this article can be found online at <https://doi.org/10.1016/j.jhevol.2019.03.015>.

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