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ORIGINAL ARTICLE

Wood Charcoal from Border Cave's Member 1RGBS: Evidence for the Environment and Plant Use During MIS 5

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Abstract We conducted an anthracological analysis of charcoal remains from Border Cave's member 1RGBS to provide environmental context for the site's occupation ca. 74 ka. Charcoal specimens were analyzed to assess their quality and quantity, and identify their tree taxa to reconstruct the vegetation communities available to the site's occupants. Specimens were analyzed using light stereomicroscopy and following standard anthracology methods. We identified the tree taxa that grow predominantly in the savanna, forest, and grassland vegetation communities. Using the current distribution of these communities as a reference, we suggest that the archaeological Border Cave landscape included vegetation types that now grow in southern Africa's interior warm parts. Our data revealed that *Tarchonanthus* sp. was collected most abundantly at this time, possibly for its medicinal and cosmetic properties. *Euphorbia* species were also collected, perhaps for their latex before their wood was burned. Furthermore, green wood logs of *Tarchonanthus* sp. were burned or discarded into the fire; this is evidenced by the high proportion of fragments of this species bearing radial cracks. There may have been unfavorable environmental conditions in the archaeological landscape that resulted in the wood vessel occlusion of many trees. These were likely episodic microclimatic conditions around the cave during some growth phases of the trees. These conditions and their intensity, however, were not fatal to the trees in this dataset.

Résumé Nous avons effectué une analyze anthracologique des restes de charbon du membre 1RGBS de Border Cave pour fournir un contexte environnemental pour l'occupation du site ca. 74 ka. Des spécimens de charbon de bois ont été analysés pour évaluer leur qualité et leur quantité et identifier leurs taxons d'arbres pour reconstituer les communautés végétales disponibles pour les occupants du site. Les échantillons ont été analysés en utilisant la stéréomicroscopie optique et en suivant les méthodes d'anthracologie standard. Nous avons identifié les taxons d'arbres qui poussent principalement dans les communautés végétales de savane, de forêt et de prairie. En utilisant la distribution actuelle de ces communautés comme référence, nous suggérons que le paysage archéologique de Border Cave comprenait des types de végétation qui poussent maintenant dans les régions intérieures et chaudes de l'Afrique australe. Nos données ont révélé que *Tarchonanthus* sp. a été récolté le plus abondamment à cette époque, peut-être pour ses propriétés mé-

Archaeological time period: Late Pleistocene—74 thousand years ago; Country and region discussed: South Africa, south-east/KwaZulu Natal province

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dicinales et cosmétiques. Les espèces d'*Euphorbia* ont également été récoltées, peut-être pour leur latex avant que leur bois ne soit brûlé. De plus, des bûches de bois vert de *Tarchonanthus* sp. ont été brûlés ou jetés dans le feu ; ceci est mis en évidence par la forte proportion de fragments de cette espèce présentant des fissures radiales. Il peut y avoir eu des conditions environnementales défavorables dans le paysage archéologique qui ont entraîné l'occlusion des vaisseaux en bois de nombreux arbres. Il s'agissait probablement de conditions microclimatiques épisodiques autour de la grotte pendant certaines phases de croissance des arbres. Ces conditions et leur intensité, cependant, n'ont pas été fatales aux arbres de cet ensemble de données.

Keywords *Tarchonanthus* sp. · *Euphorbia* sp. · Climate · Charcoal · Green wood · Vessel occlusion

Introduction

Border Cave is a repository of rare prehistoric finds that have taught us about Middle Stone Age (MSA) human cultural innovations dating back to 200 ka (Backwell et al., 2018). The cave was recently revisited to gain a more refined understanding of the archaeological finds from the excavations conducted between 1940 and 1978 (Backwell et al., 2018). Central to the aim of the current investigation is the need to clarify the spatial and temporal context for the evolutionary milestones and innovations for which the site is known. This paper provides the palaeoenvironmental context and vegetation history of the site's occupation and the introduction of Howiesons Poort lithic technology during a critical point in the late Pleistocene. The Howiesons Poort lithic industry at Border Cave began ca. 74 ka at the time when global climate was undergoing a gradual transition from Marine Isotope Stage (MIS) 5 to MIS 4, a period of many environmental upheavals, including the super-eruption of Mount Toba in Indonesia (Ambrose, 1998). This period, therefore, begs for a careful assessment of the key elements that played a role in shaping the landscape on which people lived. In this study, wood charcoal is studied to identify the taxa of the remnant trees and interpret the environment under which late Pleistocene vegetation grew. In addition, the patterns of use of wood/vegetation by human groups who visited the cave will also be determined.

Charcoal remains are recovered in abundance from many MSA archaeological sites and are used, in conjunction with other environmental proxies, to reconstruct past climates, vegetation histories, and evidence of wood use (Cartwright, 2013; Cartwright et al., 2014; Esterhuysen & Mitchell, 1996; House & Bamford, 2019; Lennox & Bamford, 2015). Anthracological studies have focused intensely on using wood anatomy to describe broad changes in climate and vegetation, taking full advantage of the sensitivity of the species-diverse woody vegetation to the many climatic zones of southern Africa (Allott, 2006; Cartwright et al., 2014; Esterhuysen et al., 1999; Lennox & Wadley, 2019). This is allowed by the adaptive traits of trees that make each species thrive in a limited range of climatic conditions and, therefore, make them excellent climate proxies. Anatomical traits of some species, such as vessel diameter and growth rings, can also be used to understand fluctuations in rainfall in temperate regions (Limier et al., 2018; Terral & Mengual, 1999). The same method has been recommended in southern Africa using *Combretum apiculatum* and *Protea caffra* (February, 1993).

A qualitative analysis of charcoal in southern Africa was recently conducted by the authors using charcoal from Sibudu Cave (Zwane & Bamford, 2021). This study proved that, apart from wood microfeatures, there are environmental attributes or traces of microorganisms that may have been preserved in the wood structure. These may inform about tree mortality and the enduring microclimatic conditions that did not necessarily alter vegetation makeup. These details are seldom preserved in other botanical remains and increase the potential for charcoal to answer a wide range of questions about past human-plant-environment interactions, notwithstanding the biases that are introduced by the wood selection, thermal decomposition, site formation, and taphonomic processes. (Chrzazvez et al., 2014; Marston, 2009; Théry-Parisot et al., 2008). Therefore, a qualitative approach is applied in this study to assess for wood degradation and evidence of wood-dwelling organisms that could inform about the immediate environment of the landscape near the site. These may be interpreted from structural deformation, non-anatomical residues, and non-organic inclusions in the wood structure of the trees.

Site Setting and Excavation

Border Cave is situated at the bottom of the eastern escarpment of southern Africa at the border of South Africa (KwaZulu Natal Province) and Eswatini (Swaziland). The cave, located 82 km from the Indian Ocean, is carved into a cliff that towers 678 m above sea level (Fig. 1). It was formed in the Lower Jurassic volcanic rocks, named the Jozini Formation of the Lebombo Group (Backwell et al., 2018). The vegetation near the site is suited to tropical climatic conditions (Mucina & Rutherford, 2006). These are mostly trees, shrubs, climbers, and grasses that make up the closed, wooded habitat of the southern Lebombo Mountains. The topography of the cave locality is a steep, leeward slope of the mountains and, therefore, subject to the rain shadow of the orographic precipitation that is promoted by the warm currents of the Indian Ocean (Beal et al., 2011). The contemporary vegetation around the cave belongs to the Lowveld unit of the Savanna Biome and currently features small patches of forests at some distance from the cave (Mucina & Rutherford, 2006).

There are approximately 300 woody plant species that have been noted near Border Cave since the 1970s. These include 214 species identified by John Anderson (Beaumont, 1978) and more than 60 identified by other botanists (Backwell et al., 2018; Mucina & Rutherford, 2006). Some of the most common woods include many species that belong to these families: Fabaceae, Anacardiaceae, Combretaceae, Euphorbiaceae, and Ebenaceae (Backwell et al., 2018; Beaumont, 1978; Mucina & Rutherford, 2006). The overrepresentation of the taxa in these families may be driven by the influence of the prevailing climatic conditions on the landscape, as is common with many vegetation communities of southern Africa.

Previous excavations (1940–1970) revealed three distinct lithic technologies in the MSA sequence and are originally termed the Pietersburg, Epi-Pietersburg, and post-Howiesons Poort (Beaumont, 1978; Cooke et al., 1945). These have been re-classified into the early MSA (MSA1), Howiesons Poort, and post-Howiesons Poort Industries (Backwell et al., 2018; Lombard et al., 2012). The industries were recovered from the archaeological deposit with alternating sand

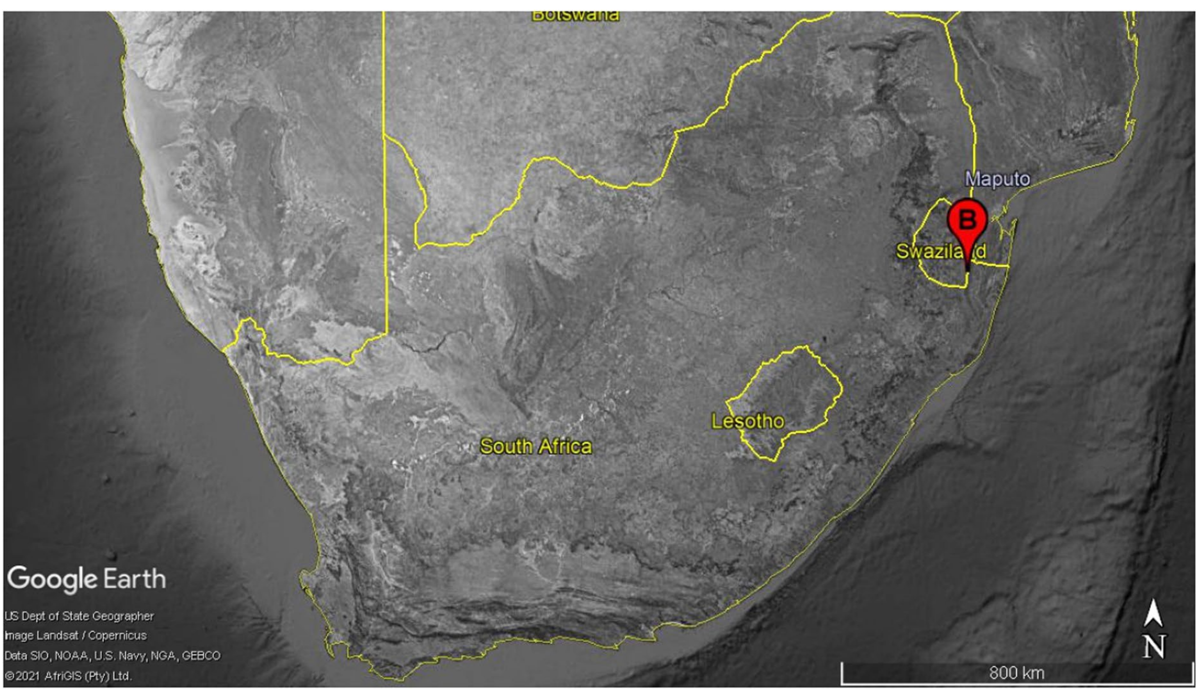


Fig. 1 The location of Border Cave in southern Africa along the border of South Africa and Eswatini (Swaziland)

and ash layers/members dated between 44 and 220 ka (Backwell et al., 2018; Grün & Beaumont, 2001). Since Beaumont's (1978) excavation, these members have been carefully re-excavated following their natural stratigraphy and named after the texture and color of their dominant sediments (Backwell et al., 2018). The first Rubbly Grey-Brown Sand (1RGBS) member is lodged underneath the third White Ash member (3WA) and lies on top of the fourth Brown Sand member (4BS). The sediments of member 1RGBS, dated through Electron Spin Resonance (ESR) to ~ 74 ka, are dominated by brown sand-sized particles that accumulated at a lower rate than those of member 3WA (64 ka) above, however, at a similar rate to the preceding member 4BS (77 ka) (Backwell et al., 2018; Beaumont, 1978; Grün & Beaumont, 2001).

The occupational phase corresponding to member 1RGBS marks the beginning of Howiesons Poort lithic industry, a technology that continued until 64 ka, i.e., in 3WA (d'Errico & Backwell, 2016). During Cooke et al.'s (1945) excavation of the site, remains of an anatomically modern human infant were recovered with grave goods from member 1RGBS (d'Errico & Backwell, 2016). These represent the earliest known evidence for funerary practices involving symbolic behavior in Africa (Cooke et al., 1945; d'Errico & Backwell, 2016; Rightmire et al., 1979). Despite yielding a well-preserved infant skeleton and the Howiesons Poort lithic industry, little is known about the environment associated with the deposition of member 1RGBS. The marine gastropod shells, *Conus ebraeus*, which were buried with the infant and identified as ornaments/grave goods, suggest the presence of warm ocean waters in the nearby Indian Ocean (d'Errico & Backwell, 2016). These warm conditions complement the warm sea surface temperatures that have been interpreted from $\delta^{18}O$ of the foraminifera from the coast of Mozambique (Caley et al., 2011) as well as warm and dry terrestrial conditions at the end of MIS 5a, previously suggested through the analysis of soil sediments from the cave (Butzer et al., 1978).

New excavations at Border Cave, which yielded the charcoal materials discussed in this article, commenced in 2015 under the directorship of Lucinda Backwell, Francesco d'Errico, and Lyn Wadley. The charcoal remains were recovered from 1RGBS with many artifacts that were deposited anthropogenically, including lithic tools, faunal remains, shell fragments, and botanical remains. There are also naturally deposited soil sediments and fragmented cave spall. These are all valuable materials from which cultural and environmental data can be interpreted (Backwell et al., 2018; Beaumont, 1978). These findings indicate that, like the occupants at different times during the MSA, the makers of the Howiesons Poort lithic technology foraged over a wide range of habitats and had complex economic, ethical, and esthetic systems (Backwell et al., 2018; Beaumont, 1978).

Evidence for the exploitation of plants at the site date as far back as 200 ka in the form of combustion features, including the earliest evidence for the use of grass bedding (Wadley et al., 2020a) and the consumption of cooked geophytes at 170 ka (Wadley et al., 2020b). The transition between the different MSA lithic technologies and their respective foraging strategies provides an important insight into modern human behavioral evolution, comparable with other MSA human activities in Africa (Backwell et al., 2018; Beaumont, 1978; d'Errico & Backwell, 2016). Furthermore, the temporal and environmental settings of these MSA contexts provide a way to understand behavioral trends that may have responded to stresses experienced on a local and global scale, including significant major climatic events.

Methods and Materials

Charcoal fragments were excavated from member 1RGBS in 2018 and 2019. Fragments were subsampled into a smaller assemblage, systematically chosen from different size classes ranging from ~ 0.3 to 2.5 cm. The appearance of new taxa was tracked using the cumulative frequency or saturation curve (Fig. 2). Charcoal fragments were manually fractured for microscope analysis, carefully exposing the three sections: Transverse section (TS), Tangential Longitudinal Section (TLS), and Radial Longitudinal Section (RLS), for a detailed study of the microanatomy of wood (Wheeler et al., 2007). The wood microstructure was examined using an Olympus light stereomicroscope fitted with objective lenses, up to 500 × magnification. The Olympus Image Analysis software was used for taking digital photographs, counting, and measuring microfeatures.

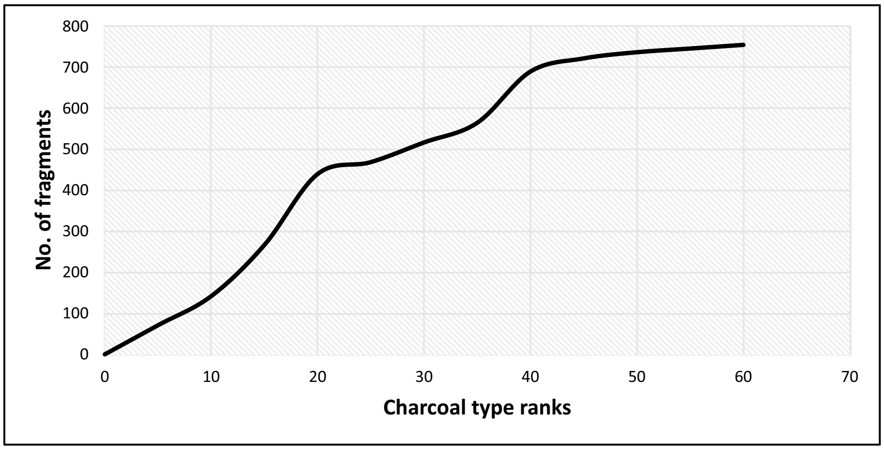


Fig. 2 The cumulative frequency of charcoal fragments against the types/taxa from member 1RGBS of Border Cave

All the charcoal fragments were captured digitally, and their micrographs are kept at the Evolutionary Studies Institute's database. The taxonomic identification of wood remains was made following the standard procedure recommended by the International Association for Wood Anatomists (IAWA) as well as by comparison with many different species from southern Africa (Dechamps, 1993; Kromhout, 1975), including those in the InsideWood online database (https://insidewood.lib.ncsu.edu). The Evolutionary Studies Institute herbarium houses more than 600 woody specimens collected from many parts of southern Africa and representing more than 400 different woody species. Most of these species were collected by various researchers from many parts of southern Africa (Allott, 2005; Chikumbirike, 2014; Zwane, 2018) and included more than 30 species recently collected by Sandra Lennox, University of the Witwatersrand, from the vicinity of Border Cave.

Most charcoal studies in southern Africa have refrained from quantifying woody species identified in an assemblage based on the number of charcoal fragments analyzed. Instead, they have opted to use the presence of species (or a group of species) which are indicative of vegetation communities, a method that works best for the diverse flora of southern Africa (Cartwright & Parkington, 1997; Cartwright et al., 2014; Esterhuysen & Mitchell, 1996; February, 1992; Lennox & Wadley, 2019). For example, Cartwright has rejected the idea that the number of charcoal fragments can indicate relative abundance of different species present or even collected in the past (Cartwright & Parkington, 1997). The fragment abundance of some species over others can, however, be statistically relevant, as demonstrated by February (1992), provided that sampling methods include wood fragments of all sizes in an assemblage (Byrne et al., 2013; Dotte-Sarout et al., 2014). It has been proven that the relative abundance of fragments could reflect the relative abundance of species, regardless of individual species' wood properties. However, this has not been accepted by all researchers. Experimental work supporting this suggestion showed that despite differences in physical characteristics of wood, archaeological charcoal assemblages reflect the record of the woody species originally burned, although the least represented/collected woods are most likely preserved through very small fragments (Byrne et al., 2013; Dotte-Sarout et al., 2014). Such studies have contributed toward estimating a minimum number of fragments required for analysis to achieve a representative sub-set, especially in regions with a temperate climate.

In southern Africa, the minimum number of fragments needed for a representative charcoal sample has not been determined. This problem is complicated by the fact that even when using saturation curves to sub-sample a representative assemblage, a clear plateau of the curve is barely reached in southern Africa, as in other regions with high species diversity (Fig. 2; Dotte-Sarout et al., 2014; Zwane & Bamford, 2021). Nevertheless, such studies are needed, first, to standardize charcoal analyses with international norms and consider the unique diversity of major vegetation communities in the subcontinent; and second, to determine an accurate measure of ecological representativeness of woody vegetation in the past. Overall, these studies are useful for interpreting the abundance of some taxa over others based on fragment frequencies in archaeological contexts. This quantitative interpretation method is used alongside the species presence/absence approach to interpret the results of the charcoal dataset from Border Cave.

Results

Sample Reliability and Taphonomy

So far, new excavations have removed about 77 L of archaeological sediments from 1RGBS and yielded more than 3000 charcoal fragments from which the assemblage in this study was subsampled. These fragments come from three squares (N108 E117; N108 E116, and N109 E117), each measuring approximately 1×0.5 m. The member 1RGBS comprises two sub-layers: FAAN, from which 68.5 L of archaeological deposit were removed, and lies stratigraphically below FEBA, whose deposit comprises only 8.5 L (Lucinda Backwell, email correspondence, 18 November 2020). Layer FEBA had 942 charcoal fragments from which 296 were subsampled; while 600 were subsampled in layer FAAN with a total of 2,252. Most charcoal fragments were very well preserved and could be studied in detail for taxonomic identification. Only 141 samples were too small, or pith, knot, and crumbly fragments, and could not be identified taxonomically. The remaining 755 samples were grouped into 57 taxa/types based on the similarities in their wood microstructure. Approximately, 65% (n=37) of these types were identified to genus or species (Table 1 and Supplementary Material). Charcoal fragments in this study were not recovered from hearths or fireplaces; instead, they represent disturbed hearth debris from many burning events in the cave scattered over the excavated area (Théry-Parisot et al., 2008). This assemblage gives a more representative sub-set of woody vegetation that was collected and burned during many different occupational periods, probably across several decades leading to 74 ka, rather than a few burning events that are commonly marked by intact hearths (Dotte-Sarout et al., 2014; Théry-Parisot et al., 2008).

Charcoal fragments per type/taxa ranged between 1 and 123 and had a mean of 13 fragments per type/taxon (Table 1). Two outliers stood out: *Tarchonanthus* sp. and *Euphorbia* sp. 1 with 123 and 80 fragments, respectively. The over-representation of the two species suggests that they were collected more than others in the past. Six species: *Brachylaena huillensis*, *Colophospermum mopane*, *Combretum krausii*, *Euphorbia* sp. 2, *Ozoroa paniculosa*, and *Searsia lancea* were identified only from sub-layer FAAN, while *Protea* sp. 1 and *Sterculia rogersii* were restricted to FEBA (Fig. 3). This distribution pattern could be a direct consequence of the duration or rate of sediment accumulation of the sub-layers since FAAN is significantly thicker than FEBA (Lucinda Backwell, email correspondence, 18 November 2020). The implication of this is that the cave was occupied more frequently or over a longer period during the deposition of FAAN than FEBA. There were 29 species that were common to both FEBA and FAAN sub-layers, but more fragments within each species were found in FAAN than in FEBA, perhaps, due to depositional bias (Fig. 3).

The Identification of Euphorbia Species

Comparative Euphorbia tirucalli and Archaeological Euphorbia sp. 1 (Type 37)

Wood samples of *E. tirucalli* were collected by Lennox (SJL171) near Border Cave and, with permission, carbonized by the authors. The description of wood anatomical features of this specimen compares very well with a description of the same species on InsideWood. On the Traverse Section (TS), the vessel arrangement is mostly solitary and has few short radial multiples; the fibers are distinctly thin, and the parenchyma cells are diffuse (Fig. 4a). On the Radial Longitudinal Section (RLS), the ray cells of this species are mixed throughout (Fig. 4b). When observed from the Tangential Longitudinal Section (TLS), the rays are uniseriate to triseriate, and the width of the biseriate and triseriate portions is the same as that of the uniseriate cells (Fig. 4d). The length of these rays varies; however, they are generally less than 1 mm. The characteristic presence of laticifers or latex tubes was noted in the enlarged parts of the rays, indicated by an arrow in Fig. 4c, a common phenomenon in species belonging to the genus *Euphorbia* (Mennega, 2005).

In archaeological charcoal fragments identified to *Euphorbia* sp. 1 (Type 37), vessels are arranged more often in short radial multiples than solitarily on the TS (Fig. 5a). The TS surface is also distinctly defined by thin fibers and diffuse parenchyma cells. The upright, procumbent, and square ray cells of

Table 1 The list of species identified from Border Cave showing the taxa and number of the identified types, the total number of charcoal fragments per taxon, the number of fragments in each sub-layer; as well as fragments with radial cracks, brown deposits, white deposits, and blue-yellow stains in the wood structure per taxon. Cf. marks the species or genera that were identified with less certainty

Taxa		Type no	Total no. fragments	Sub-layers		Fragments w/ cracks	Fragments w/ brown deposits	Fragments w/ white deposits	Fragments w/ stains
Species and authorship	Family			FEBA	FAAN				
Allophylus sp.	Sapindaceae	39	3	2	1	0	1	0	0
Apodytes dimidiata E.Mey. ex Arn	Icacinaceae	26	10	4	6	1	2	0	0
Brachylaena cf. *discolor* DC	Asteraceae	34	11	3	8	8	0	0	0
Brachylaena huillensis O.Hoffm	Asteraceae	50	2	0	2	0	2	0	0
Chionanthus battiscombei (Hutch.) Stearn	Oleaceae	19	24	12	12	1	8	0	3
cf. *Chionanthus foveolatus* (E.Mey.) Stearn	Oleaceae	4	5	2	3	2	0	0	0
Colophospermum mopane (J.Kirk ex Benth.) J.Kirk ex J.Léonard	Fabaceae	57	2	0	2	1	1	0	1
Combretum krausii Hochst	Combretaceae	56	7	0	7	0	1	1	2
Dichrostachys cinerea (L.) Wight & Arn	Fabaceae	43	7	2	5	1	1	0	0
Diospyros dichrophylla (Gand.) De Winter	Ebenaceae	9	35	13	22	2	19	1	8
Diospyros natalensis (Harv.) Brenan	Ebenaceae	46	4	1	3	1	0	0	0
Euphorbia sp. 1	Euphorbiaceae	37	80	13	67	1	51	5	15
Euphorbia sp. 2	Euphorbiaceae	48	2	0	2	0	0	0	1
Gymnosporia nemorosa (Eckl. & Zeyh.) Szyszyl	Celastraceae	33	3	1	2	0	0	0	1
cf. *Heywoodia lucens* Sim	Phyllanthaceae	2	19	7	12	0	3	0	1
Lannea discolor (Sond.) Engl	Anacardiaceae	38	9	3	6	0	3	0	4
Maytenus sp.	Celastraceae	36	24	13	11	7	2		2
Mystroxylon aethiopicum (Thunb.) Loes	Celastraceae	14	6	3	3	0	1	0	0
Ozoroa cf. *paniculosa* (Sond.) R.Fern. & A.Fern	Anacardiaceae	44	6	0	6	2	0	0	1
Podocarpus/ Afrocarpus sp.	Podocarpaceae	20	14	7	7	0	0	0	2

Table 1 (continued)

Taxa: Species and authorship	Taxa: Family	Type no	Total no. fragments	Sub-layers: FEBA	Sub-layers: FAAN	Fragments w/ cracks	Fragments w/ brown deposits	Fragments w/ white deposits	Fragments w/ stains
Protea cf. *roupelliae* Meisn	Proteaceae	41	3	2	1	0	0	0	0
Protea sp. 1	Proteaceae	22	1	1	0	0	0	0	0
cf. *Protea* sp. 2	Proteaceae	49	2	1	1	0	0	0	2
cf. *Rauvolfia caffra* Sond	Apocynaceae	5	19	8	11	3	6	3	2
Sclerocarya birrea (A.Rich.) Hochst	Anacardiaceae	32	11	4	7	3	1	1	6
Searsia chirindensis (Baker f.) Moffett	Anacardiaceae	55	2	1	1	0	0	0	0
Searsia lancea (L.f.) F.A.Barkley	Anacardiaceae	47	4	0	4	1	2	0	2
Senegalia ataxacantha (DC.) Kyalangaliwa & Boatwr	Fabaceae	25	9	2	7	0	3	0	2
Senegalia caffra (Thunb.) P.J.H.Hurter &Mabb	Fabaceae	42	8	1	7	1	1	1	1
Senegalia sp.	Fabaceae	3	17	4	13	2	0	3	1
Sterculia sp.	Sterculiaceae	24	1	1	0	0	1	0	0
Tarchonanthus sp.	Asteraceae	18	123	38	85	59	4	5	13
Vachellia robusta (Burch.) Kyalangalilwa & Boatwright	Fabaceae	40	9	2	7	1	1	0	1
Vachellia sieberiana (DC.) Kyal. & Boatwr	Fabaceae	1	11	5	6	1	5	1	1
Vachellia sp. 1	Fabaceae	12	4	3	1	0	3	0	1
Vachellia sp. 2	Fabaceae	23	6	2	4	0	4	1	3
Vachellia tortilis (Forssk.) Gallaso & Banfi	Fabaceae	31	10	1	9	0	3	1	0
Undetermined types/ fragments	Undetermined	-	231	107	135	47	37	14	39

this specimen on the RLS are mixed, i.e., irregular cell arrangement throughout the rays (Fig. 5b). These rays appear mostly uniseriate and biseriate on the TLS; and similar to *E. tirucalli*, the widths of biseriate portions are equal to the uniseriate cells of the rays (Fig. 5d). Laticifers or latex tubes (arrow in Fig. 5c) were also noted in the fragments belonging to this type in the archaeological assemblage.

Three dissimilarities were noted between the comparative sample of *E. tirucalli* and the archaeological *Euphorbia* sp. 1. The first is the vessel arrangement on the TS (i.e., abundance of solitary vs. short radial multiple). Secondly, the average ray length (i.e., the ray height in both samples) varies from < 0.5 to 1 mm (Figs. 4d and 5d). In contrast, a reliable description of *E. tirucalli* on InsideWood records that the ray height of this species

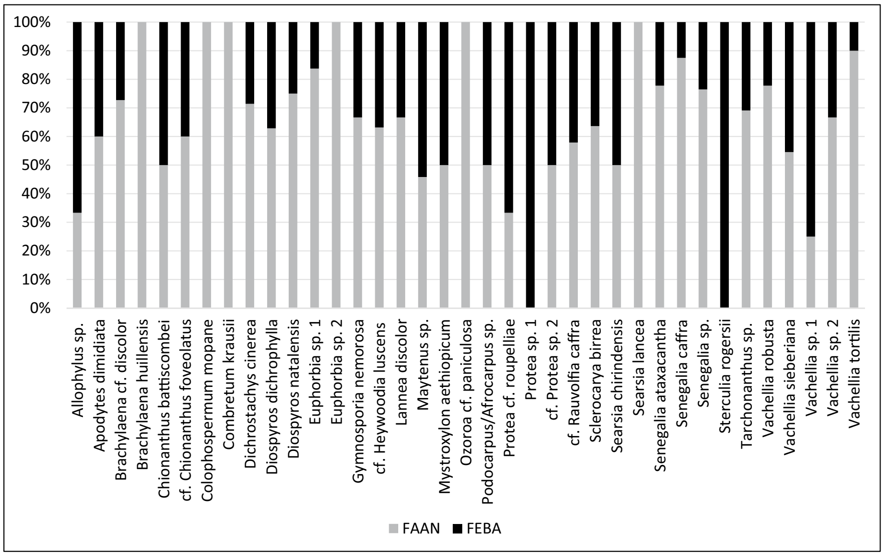


Fig. 3 The abundance of species in sub-layers FAAN and FEBA within member 1RGBS

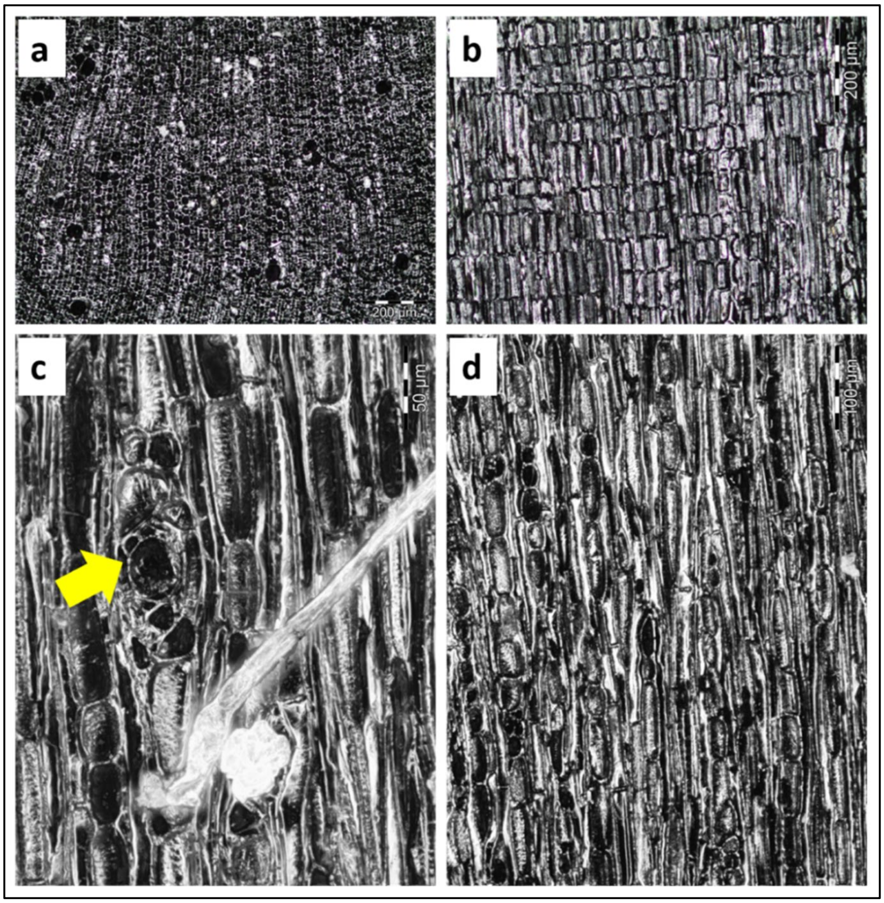


Fig. 4 The micrographs of *Euphorbia tirucalli* from the modern Border Cave landscape showing the wood anatomy along the TS (**a**), TLS (**b**), and RLS (**c**, **d**). Scale bar on (**a**) and (**b**) = 200 µm, (**c**) = 50 µm, and (**d**) = 100 µm

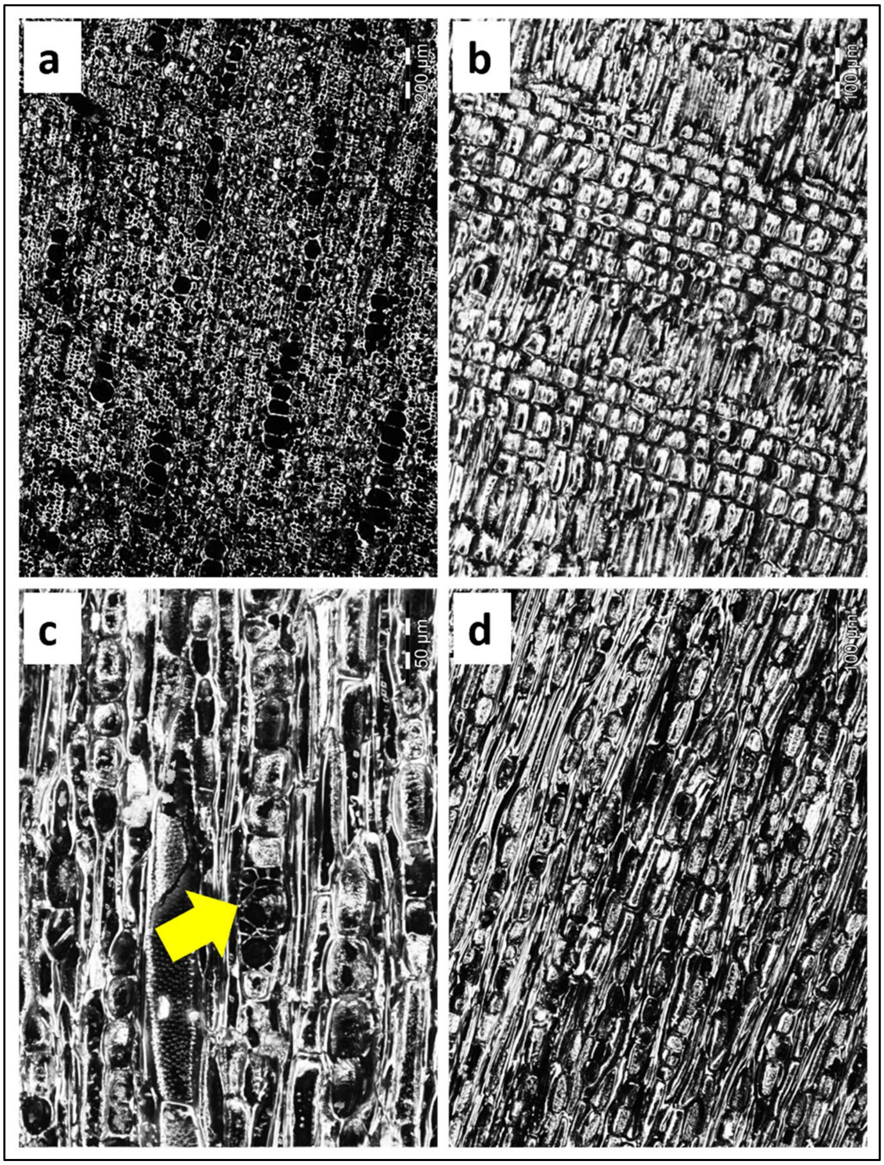


Fig. 5 The micrographs of *Euphorbia* sp. 1 from the archaeological Border Cave landscape showing the wood anatomy along the TS (**a**), RLS (**b**), and TLS (**c**, **d**). Scale bar on (**a**) = 200 µm, (**b**) and (**d**) = 100 µm, and (**c**) = 50 µm

may reach up to > 1 mm. The third dissimilarity was the presence of prismatic crystals in the fibers of *E. tirucalli*, not noted in the archaeological specimens of *Euphorbia* sp. Prismatic crystals occur in many genera of Euphorbiaceae, including *Spirostachys* (Lennox & Bamford, 2015), but they were not visible in the archaeological specimens in question. Nevertheless, this taxonomic identity was confirmed based on many similarities that the archaeological fragments of this second most abundant archaeological type share with the general description of some *Euphorbia* species.

Euphorbia sp. 2 (Type 48) in Archaeological Assemblages

The 48th type in the archaeological assemblage was identified to *Euphorbia* sp. 2 following the description of *E. candelabrum* on InsideWood and Mennega (2005). The most important wood microfeatures found in this species include less frequent (5–20/mm^2), wide (100–200 µm), and long vessels (350–800 µm), which have large gash-like or scalariform inter-vessel pits (Fig. 6a–c). These occur

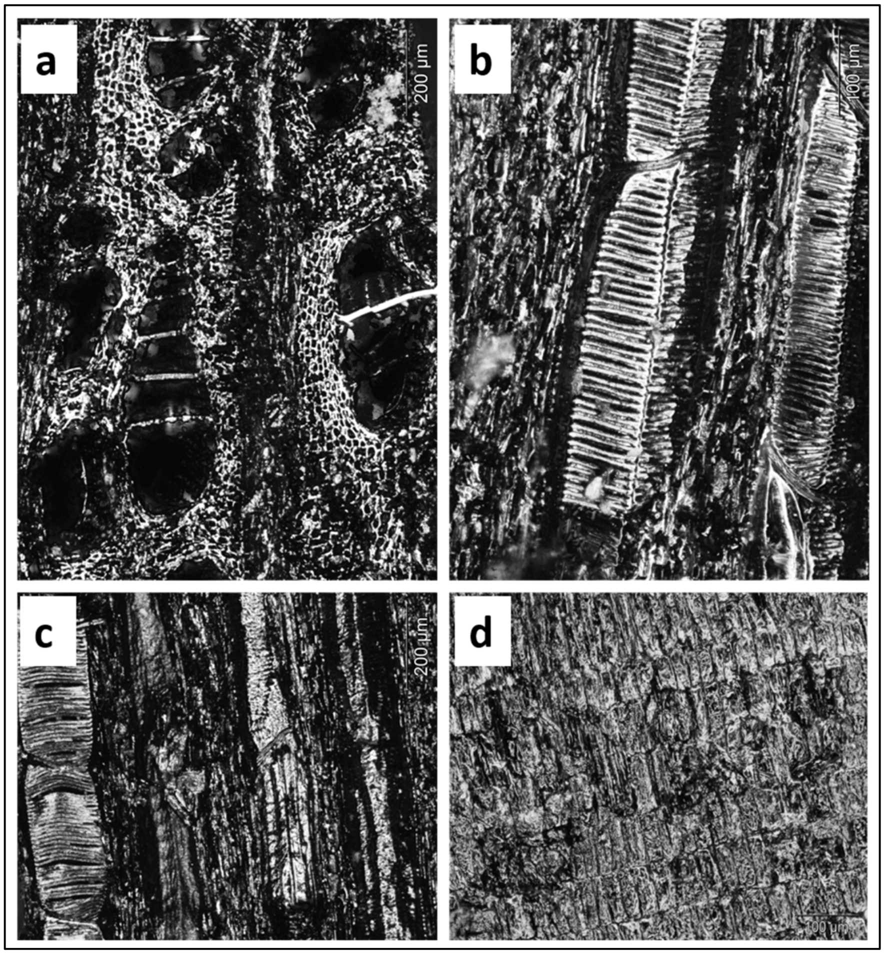


Fig. 6 The wood anatomy of archaeological fragment belonging to *Euphorbia* sp. 2 showing the TS (**a**, **c**), TLS (**b**), and RLS (**d**). Scale bar on (**a**, **c**) = 200 µm and (**b**, **d**) = 100 µm

with exclusively uniseriate and short rays (< 0.5 mm) whose cells are homocellular upright on the RLS (Fig. 6d). The authors did not study comparative specimens of this species. However, the descriptions published by the two sources were enough to confirm that there may be a second *Euphorbia* species in the archaeological dataset. This is based on the presence of important vessel and ray characteristics, including scalariform inter-vessel pits similar to those found in some *Euphorbia* species such as *E. ingens*.

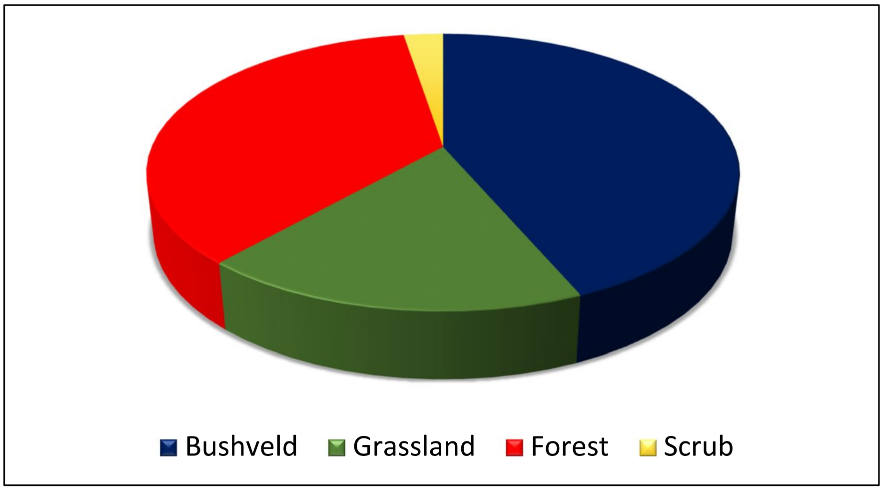
Vegetation Communities Represented by the Species

Four vegetation communities were identified from the charcoal types/species in the archaeological Border Cave landscape. These are, in the order of dominance, Bushveld (43.5%), Forest (36%), Grassland (18%), and Scrubland (2.5%) communities (Fig. 7). These communities are based on the modern distribution of the species. Therefore, it is possible that scrubland vegetation did not comprise a significant portion of the vegetation near the cave because it is so scarcely represented in this fraction of archaeological woody vegetation.

Wood Vessel Occlusion by Unknown Residues

A significant proportion of fragments in many different charcoal types had strange residues of different colors and textures, mostly inside vessel elements. These residues were recorded in three categories: brown deposits, white deposits, and blue-yellow stains (Table 1). Brown residues are always found deposited inside wood vessels where they appear like a stringy mass and sometimes granular. These residues were observed in 166 fragments belonging to 39 types/species (Fig. 8). Most of the fragments (63%) belonging to *Euphorbia*

Fig. 7 The proportions of all vegetation communities in member 1RGBS



sp. (Type 37) contained much of the brown deposits (Fig. 9a). White residues were noted and often appear like a solid mass inside the vessels of 32% of all 57 taxa (Figs. 8 and 9b). Blue-yellow stains were also seen in the vessels and tyloses of species such as *Sclerocarya birrea*, and in the phloem of *Combretum krausii* (Fig. 9c). Except for blue-yellow stains, the brown and white residues were restricted to some growth rings/growth phases of the woody vegetation in this assemblage (Fig. 9a and b). The nature of these deposits in the wood is not yet fully understood, but it is possible that they were produced sporadically by the trees and shrubs or by other unknown organisms in the habitats of the different species. Insect burrows containing insect frass were also present in seven fragments that belong to four types/species in this dataset.

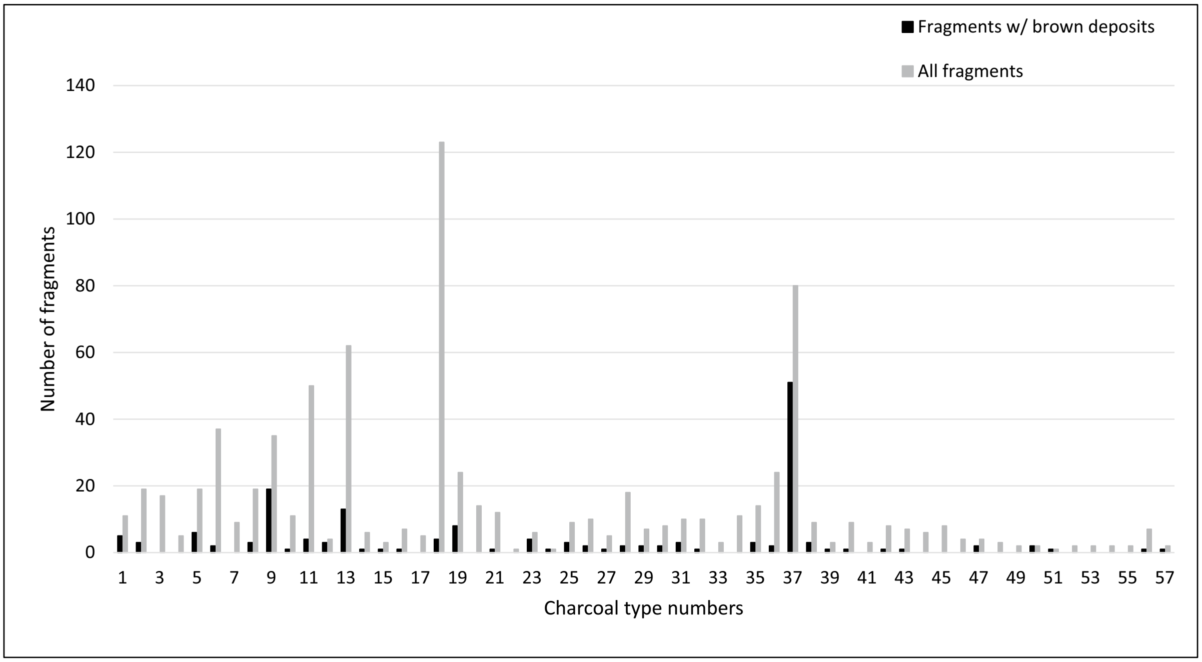
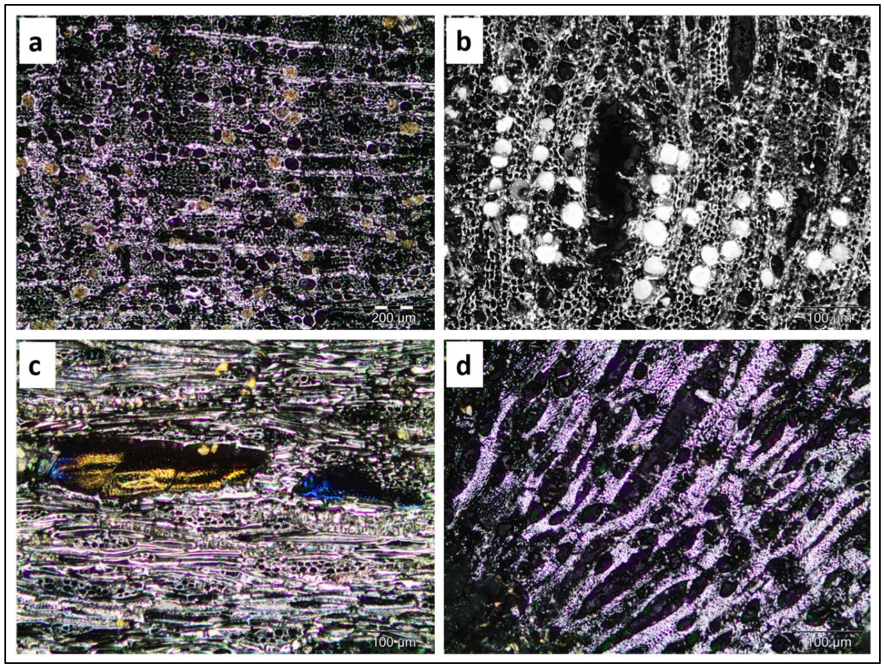


Fig. 8 The abundance of fragments with brown deposits inside vessels and the total number of fragments per type

Fig. 9 Examples of wood fragments containing brown deposits (**a**), white deposits (**b**), and blue-yellow stains (**c**) in vessels of the wood, and an example (**d**) of radial cracks viewed on the TS. Scale bar on (**a**) = 200 µm, (**b**, **c**), and (**d**) = 100 µm



Radial Cracks

Radial cracks were also noted in the fragments of 26% of the 57 taxa (Fig. 9d). These linear openings/cracks along wood rays are formed under unique conditions that possibly depended on many factors, such as exposure to heat, but are always directly related to moisture contained in the wood (Caruso Fermé et al.,

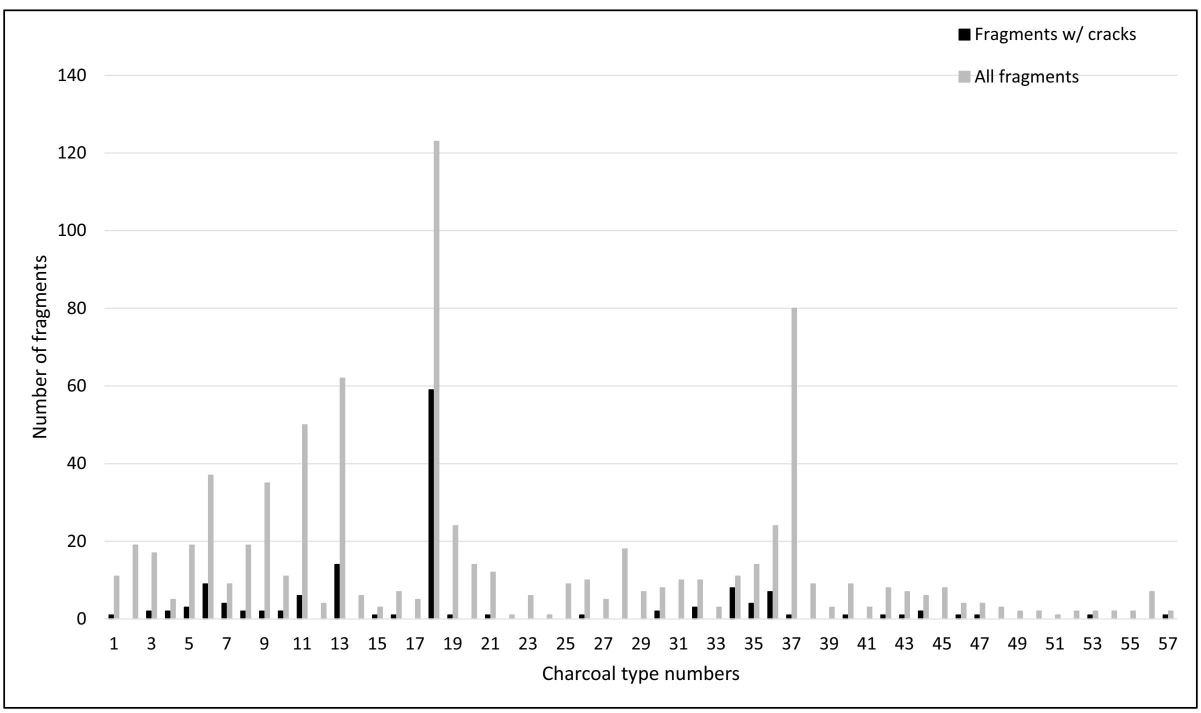


Fig. 10 The abundance of fragments with cracks and the total number of fragments per type

2018). When moisture is heated in the wood, there is a rapid increase in temperatures; pressure builds within and is released through the weak zones, commonly through ray parenchyma (Caruso Fermé et al., 2018; Théry-Parisot et al., 2010). This phenomenon is commonly associated with wood containing high amounts of moisture, such as freshly harvested or greenwood. Some species in this assemblage, including *Tarchonanthus* sp., have fragments whose wood logs were possibly burned as greenwood (Fig. 10).

Discussion

The Bushveld vegetation, otherwise known as Savanna Biome vegetation, grows on diverse habitats and soil substrates that receive varying amounts of precipitation. These vegetation communities are divided into many units and are described by Mucina and Rutherford (2006). At Border Cave, two Lowveld Savanna units (SVl 16 and 17) dominate the modern landscape, but there is also some montane forest vegetation. It appears that more Savanna vegetation communities are present due to many changes in the climate, which allowed for the growth and expansion of different species. Approximately 43% of the species identified at Border Cave 74 ka, including seven different *Senegalia* and *Vachellia* species (formerly known as *Acacia*), are characteristic Savanna woods. Through these species, three Savanna vegetation units were recognized: Mopane, Sub-escarpment, and Lowveld. The Mopane (SVmp 2) unit, currently found several kilometers west of the site, is represented by *Sclerocarya birrea*, *Colophospermum mopane*, *Vachellia tortilis*, and *Sterculia rogersii*. The Sub-escarpment (SVs) is signified by *Vachellia tortilis*, *Sclerocarya birrea, Dichrostachys cinerea*, *Combretum* species, and several *Euphorbia* species (Mucina & Rutherford, 2006). They suggest that favorable conditions for these taxa were much closer to the cave than today.

Taxa such as *Brachylaena discolor*, *Diospyros dichrophylla*, *Dichrostachys cinerea*, *Sclerocarya birrea*, and *Sterculia rogersii*, as well as species belonging to *Vachellia*, *Senegalia*, *Combretum*, *Euphorbia*, *Ozoroa*, and *Lannea* genera, are commonly found in many Lowveld (SVl) units as currently seen today (Mucina & Rutherford, 2006). Forest vegetation types, Scarp and Lowveld riverine forest, were noted in the Border Cave landscape. The Scarp Forest (FOz 5), which currently borders some Lowveld units of the Savanna Biome, was present in the archaeological landscape, as indicated by *Podocarpus/Afrocarpus* sp. and cf. *Heywoodia lucens* (Mucina & Rutherford, 2006). The Lowveld riverine forest (FOa1) is represented by cf. *Rauvolfia caffra* and has many species within the *Combretum*, *Vachellia*, *Senegalia*, and *Diospyros* genera (Mucina & Rutherford, 2006).

There was also a significant proportion of Grassland woods near Border Cave. *Tarchonanthus* sp., *Vachellia sieberiana*, and *Protea* cf. *roupelliae* are very important constituents of two Grassland units (i.e., Mesic Highveld Grassland, Sub-Escarpment Grassland) as well as the Savanna Biome (Central Bushveld and Lowveld) of southern Africa. The presence and abundance of these species in the archaeological landscape of Border Cave place the grassland vegetation a few kilometers closer to the cave in the past than it is today (Mucina & Rutherford, 2006). The vegetation in the lower sub-layer of 1RGBS, namely FAAN, has six taxa: *Brachylaena huillensis*, *Colophospermum mopane*, *Combretum krausii*, *Euphorbia* sp. 2, *Ozoroa paniculosa*, and *Searsia lancea* that are widely distributed over inland areas of the subcontinent. Most of these taxa are still found near the cave; however, they collectively suggest that the environment most favorable for their growth prevailed during the deposition of the lower parts of member 1RGBS.

Moreover, *Euphorbia* species are widespread in southern Africa and indicate that a wide range of species grew during the accumulation of FAAN sediments but not during FEBA. Other species found in both sub-layers with a wide distribution in South Africa and the neighboring countries of Zimbabwe, Botswana, Angola, Namibia, and Mozambique include *Dichrostachys cinerea*, *Lannea discolor*, *Vachellia sieberiana*, *Vachellia tortillis*, and *Sclerocarya birrea*. In total, more than 60% of the species in this dataset are distributed similarly on and above the escarpment. Thus, they signify that the vegetation cover of the archaeological landscape was more comparable to that of the modern escarpment and plateau regions of the sub-continent than the coastal plain, which is represented by less than 20% of species, such as *Podocarpus/Afrocarpus* sp., cf. *Heywoodia lucens*, *Diospyros* spp., and *Searsia chirindensis* (Mucina & Rutherford, 2006; van Wyk & van Wyk, 2013).

The above implies that there was more Savanna mixed with Grassland vegetation that grew within the foraging distance of the site, according to the Principle of Least Effort (Asouti & Austin, 2005). Most of the tree/shrub species in the dataset are known for the usefulness of their wood more than the other plant parts. For example, *Dichrostachys cinerea* is used today for firewood; and it has hardwood, a characteristic it shares with many other species in this dataset, such as *Colophospermum mopane*, *Searsia lancea*, and *Brachylaena discolor* (Coates-Palgrave, 1981; van Wyk & van Wyk, 2013). The hardness and durability qualities of these species make them good timber wood today and suggest that the MSA people favored these trees, perhaps, for making wooden artifacts. Nine species identified in this dataset, including *Lannea discolor*, *Senegalia caffra*, and *Searsia chirindensis*, have known medicinal properties, while three species: *Sclerocarya birrea*, *Lannea discolor*, and *Vachellia tortilis* have nutritional value for which they are still harvested by people today (Coates-Palgrave, 1981; van Wyk & van Wyk, 2013).

Many different types of camphorbush trees (*Tarchonanthus* sp.) are known for their strong medicinal properties that are commonly extracted from the leaves, bark, and wood of these plants (Coates-Palgrave, 1981; van Wyk & van Wyk, 2013). The leaves are used medicinally and for cosmetics, and burning the leaves releases perfumed smoke that can repel insects (Lennox, 2016; van Wyk & van Wyk, 2013). Their wood is hard and durable; it is used to make wooden artifacts and can burn while wet. However, they are scarcely recorded as good fuelwood today (Gandar, 1982; van Wyk & van Wyk, 2013). The knowledge about the usefulness of these trees may indeed date back to the MSA in southern Africa, based on the presence of wood charcoal remains of *Tarchonanthus parvicapitulatus* in a hearth at Sibudu Cave, dated to 50–60 ka (Lennox, 2016). The abundance of the camphor bush tree fragments at Border Cave suggests that it was harvested/collected for many uses and hence was constantly sought after more than other species. It is also likely that it was burned/discarded in the fire as greenwood, perhaps after different plant parts were used, based on the presence of radial cracks in wood fragments of this plant.

Almost half of the total number of fragments (ratio = 0.48) of *Tarchonanthus* sp. have radial cracks and comprise some of the widest and most frequent cracks, indicating that most of the wood from this dataset plant was burned green. This high ratio is surpassed only by *B.* cf. *discolor*. However, this observation and comparison may not be statistically significant since the fragments per taxa in this assemblage had a very wide range, possibly due to such factors as taphonomy and the thermal decomposition of wood logs originally collected in the past. Similarly, *Euphorbia* species generally have known medicinal uses. The latex of many *Euphorbia* species is poisonous, has medicinal properties, and can repel or kill insects (d'Errico et al., 2012; van Wyk & van Wyk, 2013). However, like *Tarchonanthus* sp., this plant may have had uses in the MSA that are unknown today. For example, it is thought that the resin from *E. tirucalli* was used to bind a hafting material discovered in member 1BS-Lower during the Later Stone Age occupation of Border Cave (Beaumont, 1978; d'Errico, et al., 2012). Therefore, the use of this type of plant may have its origins in the MSA, and suggests the vast knowledge of it by the people and the availability of many different *Euphorbia* species close to the site.

The abundant presence of *Tarchonanthus* sp. and *Euphorbia* sp. 1 may hint at the need for these plants and their availability, favored by the environmental conditions that allowed them to grow and mature enough for use. These and several others in this dataset are important trees of the Savanna and Grassland Biomes. Moisture regime, soil substrates, and temperature variation on the escarpment and plateau of the sub-continent, determining factors for the distribution of vegetation forms and taxa, are very variable in both Savanna and Grasslands today. The Mesic Highveld Grassland, Mopane, Sub-Escarpment, and some Lowveld Savanna vegetation units thrive in the interior parts of southern Africa, where they tolerate extreme seasonality, including very high summer temperatures, cold winters, and low precipitation levels. These conditions contrast with those found below the escarpment in the coastal areas (Mucina & Rutherford, 2006). The mountainous terrain of the Border Cave landscape experiences orographic precipitation that promotes the growth of forest vegetation on the Lebombo Mountains; therefore, the presence of the montane forest at any period near the cave can be expected.

Despite the variable conditions to which the trees were suited at Border Cave, there may have been some unfavorable, or even hostile, conditions that resulted in the episodic or sporadic occurrence of vessel occlusion during certain growth phases of the woods in this dataset. These vessel deposits could be tyloses formed within the wood or even gums of organic origin that the plants secrete against aging or in response to freezing, drought, mechanical wounding, flooding, insect attack, or pathogen infection (De Micco et al., 2016; Schweingruber, 2007). Alternatively, they could be foreign substances, perhaps fungal remains, left in the wood cells only during the growing seasons when conditions were conducive for the associated unknown organisms to thrive in the habitats of the trees. The environmental conditions related to the production of these vessel deposits, however unknown, were not fatal to the trees because the growth phases (growth rings) with occluded vessels were followed by normal growth. There is also no clear relationship between vessel occlusion and vegetation communities; however, species such as *Euphorbia sp*. 1 and Type 9 had high ratios (0.64 and 0.54, respectively) of fragments occluded by brown vessel deposits.

Conclusion

During the deposition of member 1RGBS, the Border Cave landscape featured a warm climate with variability in some microenvironmental parameters, which differed from one rainy season to another and were responsible for periodic vessel occlusion in some taxa in this dataset. The vegetation mosaic in this archaeological landscape featured the ever-present montane forest of the Lebombo Mountains, along with Savanna Biome and Grassland Biome vegetation types. The presence of grasslands implies that the environmental conditions near Border Cave were generally more comparable to those found in the inland areas of southern Africa—warmer and drier than the coastal areas below the escarpment. These conditions may have attracted many species that are currently not very common close to the cave today, including two *Euphorbia* species. *Tarchonanthus* sp., an important species of some Grassland and Savanna vegetation types in southern Africa, was collected most abundantly, presumably for many medicinal and cosmetic uses. This is also, most likely, because it was available in abundance. The woods of this species were also discarded into fires or burned as greenwood because they can burn while damp. Whether intentional or not, this practice allowed the MSA people to exploit the medicinal properties of this plant that are released through its fumes. Similarly, it appears the MSA occupants of Border Cave harvested *Euphorbia* species for uses unknown to us.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10437-021-09448-4.

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