



Supplementary Materials for

Cooked starchy rhizomes in Africa 170 thousand years ago

Lyn Wadley*, Lucinda Blackwell, Francesco d'Errico, Christine Sievers

*Corresponding author. Email: lyn.wadley@wits.ac.za

Published 3 January 2020, *Science* **367**, 87 (2020)
DOI: 10.1126/science.aaz5926

This PDF file includes:

Materials and Methods
Supplementary Text
Figs. S1 to S3
Tables S1 and S2
References

Materials and Methods

Excavation and recovery of archaeological plant material

Border Cave, KwaZulu-Natal, South Africa (fig. S1), has been excavated by a multidisciplinary team since 2015, using standard archaeological methods. The excavation is under the directorship of Dr L. Backwell with permit # SAH 15/7645 from the KwaZulu-Natal heritage agency, Amafa. All pieces larger than 2 cm, and all special finds smaller than this, are point plotted with a Leica total station theodolite. When visible during excavation, all botanical remains were collected directly from sediment, and were laid on soft plastic film within hard plastic boxes. Each item was packed individually. Material not seen during excavation was recovered from nested 2 and 1 mm screens. All charcoal collected during excavation was checked with 10 to 40 x magnification using an Olympus SZ61 microscope. All excavated material is housed in the Evolutionary Studies Institute, University of the Witwatersrand, which is also the repository for the earliest excavation material by Dart and colleagues.

The new excavations into Members 5 BS and 4 WA were from squares N109 E113, N108 E113 and N108 E114. These are not full metre squares because they are remnants eroded from Beaumont's 1980s excavation. In Beaumont's grid they may be P16 and Q16, on the edge of the Horton pit (20). The named layers were subdivided when pavements of lithics formed a discrete floor and/or when features appeared on the sediment surface. Thus, the Pinkish White (PW) layer at the top of Member 4 WA is divided into four sub-layers, Pinkish White 1 to Pinkish White 4, and the White layer under this is divided into twelve sub-layers, White 1 to White 12 (Fig. 1B). Several combustion features rich in charcoal were excavated from Member 4 WA where most of the charred geophytes and several charred seeds were recovered.

Note regarding plant nomenclature and definitions

Plant names and attributions have been taken from the International Plant Names Index (34) and World Checklist of Selected Plant Families (35). The literature is unclear about the precise distinction between rhizomes, corms, bulbs and tubers (36) and sometimes there is contradictory nomenclature used for the same taxon described by different authors (28).

The glossary below has definitions:

Geophyte - A perennial plant with an underground food storage organ, such as a bulb, corm, tuber or rhizome (37).

Bulb – a short underground stem covered by enlarged and fleshy leaf bases containing stored food (37).

Corm – a thickened underground stem, upright in position, in which food is accumulated, usually in the form of starch (37). Corm leaf bases encircle the stem from the base (31). Corms have basal innovation (36).

Tuber – (*L. tuber*, swelling) – an enlarged short, fleshy, underground stem, such as that of the potato. Old tuber leaf bases circle only the apical part (31).

Rhizome – a more or less horizontal underground stem (37), but vertical structures occur, too, with innovation at the apex (36) and inclusion of stolons, offsets, or suckers (29).

While the definitions are at first glance straightforward, some plants resist placement in one or other category and because of this, *Hypoxis* geophytes have been variously named. The term 'rhizome' is used for the Border Cave specimens based on definitions from *Hypoxis* literature cited frequently here (28, 29), but Wiland-Szymańska (31) later replaced this name with 'tuber'.

She did this in preference to using ‘corm’ because of the difference in tunic structure of corms and tubers. As is the case in tubers, the *Hypoxis* old leaf bases circle only the apical part (31), while the rhizome base becomes senescent after apical innovation (29). *Hypoxis* is an unusual plant in many ways and tends to defy traditional literature definitions (29), not least because there is variability in the attributes of species within the genus. This has no doubt contributed to naming variability.

Study of the Border Cave rhizomes

The contexts of whole rhizomes are recorded in Table 1 and contexts of parenchyma fragments are recorded in Table S1. The whole rhizomes have been named and numbered, for example, ‘rhizome BC 1’. This numbering system must not be confused with the hominin numbering system. Where available, the catalogue number derived from total station plots is also written on the specimen box. The proximal ends, profiles and distal ends of all rhizomes were first photographed using an Olympus TD5 camera with z-stacking. Specimens rhizomes BC 6 and BC 17 are illustrated in Fig. 2. The morphology of each was then studied using an Olympus SZ61 binocular microscope at 40 x magnification. Size, shape, root position, and surface features were recorded. Specimens selected for anatomical study with scanning electron microscopy (SEM), using a Phenom Pure, were mounted on double-sided carbon tape on metal stubs, and cleaned with compressed air. The process was not destructive, there was no preparation required, and no coatings were used. Specimens chosen for SEM study were rhizomes BC 6, BC 17, BC 23, BC 29, and BC 30. Approximately 100 images were obtained for each. Particular attention was given to recording vascular bundles, xylem vessel tissue, parenchyma, root traces, and calcium oxalate crystals (raphide bundles).

Study of comparative plant material

Modern plant material was bought from nurseries or donated by nursery owners (see Acknowledgements). In addition, several collecting field trips were made in the Lebombo Mountains and in the Ndumu area at different seasons with permit # OP4367/2017 (to CS) from Ezemvelo KwaZulu-Natal Wildlife. Vouchers were made for the Kwazulu-Natal Herbarium, Durban and the CE Moss Herbarium, University of the Witwatersrand. Families collected include Amaryllidaceae, Asparagaceae, Aponogetonaceae, Araceae, Asphodelaceae, Commelinaceae, Cyperaceae, Typhaceae, Iridaceae and Hypoxidaceae (the species collected are: *Hypoxis hemerocallidea* Fisch., C.A.Mey. and Avé-Lall., *H. rigidula* Baker, *H. obtusa* Burch, ex Ker Gawl., *H. angustifolia* Lam., *H. argentea* Harv. ex Baker, and *H. filiformis* Baker). Plants that were not flowering when collected in the field, thereby needing identification beyond genus level, were planted in LW’s experimental garden in Limpopo. After flowering and identification to species, geophytes were photographed as both fresh and charred specimens, and then examined microscopically with an Olympus SZ61 for morphological and anatomical characteristics. SEM imagery was obtained for genera that seemed morphologically like the Border Cave specimens. The comparative collection of charred specimens is housed in the archaeobotanical laboratory in the School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand. Vouchers of desiccated geophytes were also examined and photographed in the CE Moss Herbarium at the University of the Witwatersrand.

Supplementary Text

Description of the Border Cave rhizomes

Morphology

All Border Cave rhizomes are charred, resulting in tissue deterioration, formation of secondary features and solidification of some vessels into a carbonised mass. Burning geophytes with moisture in them can cause splitting, called rhexigeny when the cavity walls are visibly torn (38). The Border Cave rhizomes often display radial rhexigeny from a sunken central axis on a disc-like proximal surface (Fig. 2), so they were cooked fresh, not dry. A sunken central axis is a common monocotyledonous feature, except among Iridaceae (39). The distal ends of the Border Cave rhizomes are most often convex, sometimes wrinkled, and occasionally conical. The rhizomes are tubular, globose or sub-globose in shape and do not generally exceed 18 mm either in diameter or height (and can sometimes be half that size). Most of the rhizomes preserve root cavities, sometimes partly filled with fragments of root. These occur around the circumference, or within the cortex, and appear to have had their origin just within the inner ground tissue, but this burned tissue is often highly deteriorated and difficult to recognise. Monocotyledon roots originate in the pericycle (40), but we are unable to trace the pericycle in the charred rhizomes, though the endodermis is recognisable in the form of a ring of fused cells (fig. S2). Many specimens retain traces of raised rings around their circumference (Fig. 2). Such modifications are produced by successive leaf scars (41) or by fibre.

Anatomy

Vascular structure. Vascular tissues often do not survive burning in a way that allows them to be identified (38) and they may become an amorphous carbon mass. Phloem is usually destroyed through burning and either forms a cavity or a solid mass, whereas xylem vessels are recognisable and may retain traces of tracheids (ladder-like tissue) (38). Burning has caused deterioration of the cellular structure of the Border Cave rhizomes. Nonetheless, some parenchyma is visible. The parenchyma cells are irregular shapes and sizes; they can be five to eight-sided angular cells or have smooth, oval shapes. The cell walls are 2-3 μm wide and the parenchyma cells vary in length from 60 μm to about 25 μm .

In some Cyperaceae, vascular bundles are flattened against the endodermis (42) and, while not all the Border Cave rhizome vascular bundles are against the endodermis, they circle it closely within the inner ground tissue. Vascular bundles are not always discrete in monocotyledons and may fuse with others at the edge of the central vascular cylinder, creating elongated groupings (38, 42). This may be the reason why, in some of the archaeological rhizomes, the clusters of xylem have many xylem vessels (commonly 12 to >20) (Fig. 3D). The vessel numbers vary between clusters and are difficult to count because of vessel deterioration and fluorescence caused by burning. The phloem is not recognisable probably because it formed a solid mass of carbon in the Border Cave rhizomes, but xylem is better preserved and scalariform tissue is readily visible in most cavities. Elongated groups of round or oval xylem cavities can be seen in BC 30 and also in BC 6 (Fig. 3D, fig. S3). This unusual arrangement is different from the better-known amphivasal vascular bundles or closed collateral bundles generally associated with monocotyledons. Nonetheless, a closed collateral bundle may be represented in BC 6 (fig. S3F).

Roots. The preserved root traces within the rhizomes are encased in a fibre sheath, the rhizodermis, with thickened walls and elongated cells. Such root cell structure is a characteristic of monocotyledons (43). Several types of root anatomy are visible, even within a single geophyte. To some extent a root's appearance is influenced by its size, but also by the extent of preservation after burning. Small roots may lack the parenchymatous region evident in larger ones. The rhizodermis is sometimes empty (Fig. 3B), but a few roots have xylem vessels preserved (fig. S3). Raphides (bundles of calcium oxalate crystals [see description later]), can be seen in some of the empty root cavities, but none was observed within the roots themselves. Secondary thickening root growth is absent. Thickening of the lateral walls in the root xylem cavities is scalariform (ladder-like) (fig. S3D), as is common for monocotyledons such as *Dracaena* L. spp., *Aloe* L. spp., *Gasteria* Duval spp., *Haworthia* Duval spp. (43) and *Hypoxis* L. spp. The scalariform xylem tissue of the Border Cave roots resembles xylem wall tissue seen elsewhere in the rhizomes (Fig. 3D).

Raphides. Calcium oxalate crystals (Fig. 3F) are abundant in the Border Cave rhizomes. They are bundles of needle-like crystals with pointed ends and four-sided cross-sections that fit Crowther's (44) Type 1 raphide, the most common form. The raphides, which are about 50 µm long and are oriented in the same direction in any given bundle, seem most frequent in the cortex, particularly close to the outer edge of the rhizome. Some cavities that once housed raphides are empty, and fragments are scattered on the rhizome surface. Other types of calcium oxalate crystal, for example, druses and styloids, are absent. Raphides are not destroyed during the burning process, unlike starch grains that were not observed in any of the Border Cave rhizomes, probably because starch grains are rarely preserved in charred material (45). Calcium oxalate crystals may form in any organ or tissue within a plant and the crystals act as calcium storage for the plant (46). Raphides have some taxonomic value, though their morphology may alter through time, for example, *Ornithogalum* L. spp. (Asparagaceae) raphides start as 4-sided needles, with wedge-shaped ends, and they develop into 6-sided needles (47). In *Typha* L. spp., mature crystals are hexagonal near the ends and octagonal in the centre (47). To some extent, raphide size also assists with identifications because in the Dioscoreaceae family the raphides may exceed 250 µm in length (42).

Identification of the Border Cave rhizomes

Table S2 lists selected attributes of various geophytes (36, 43, 47, 48, 59) known to occur in the Lebombo Mountains or the lowveld of eSwatini (formerly Swaziland). There are few data on anatomy of southern African geophytes and consequently many plant attributes are unknown. Nonetheless, several families can be easily eliminated from potential identifications based on the presence or absence of calcium oxalate crystal types. Cyperaceae, *Tulbaghia* L. spp. (Amaryllidaceae family), and *Chlorophytum comosum* (Thunb.) Jacques (Asparagaceae family) can be eliminated because they have no raphides. Instead of raphides, Cyperaceae have idioblasts containing phenolic substances (49). Though *C. comosum* also lacks raphides, it contains styloids and druses (47), which are absent from the Border Cave rhizomes. A prominent geophyte family in southern Africa, the Iridaceae, can be excluded, too, because Iridaceae corms lack raphides and contain styloids instead (47). Furthermore, the central stem depression evident not only in the Border Cave rhizomes, but in most monocotyledonous geophytes, is absent from Iridaceae. *Zantedeschia* Hook Baill. spp. (Araceae family) can be excluded as well because Araceae have distinctly grooved raphides (48) and the Border Cave ones are smooth. *Typha* L. spp. (Typhaceae

family) and *Ornithogalum* L. spp. (Asparagaceae family) can be excluded because their raphides have characteristically geometric shapes (47) not shared by the Border Cave rhizomes. Dioscoreaceae raphides are five times the size of Border Cave ones (47) and are also therefore inappropriate. *Aloe* L. spp. (Asphodelaceae family) can be excluded because their stems contain styloids as well as raphides. *Commelina* Plum. ex L. spp. (Commelinaceae family) have small quadratic crystals as well as raphides (50). *Commelina erecta* L., present in the Lebombo Mountains, has stem anatomy with circular or sub-circular vascular bundles, but lacks elongated ones (51). Furthermore, although the Commelinaceae family includes *Aneilema* R.Br., *Commelina* Plum. ex L., *Cyanotis* D.Don and *Coleotrype* C.B.Clarke spp. that grow in the area (52), none has a geophyte with morphology that matches the Border Cave one. Orchidaceae are protected plants and we could not collect comparative material, nonetheless, the morphology of the rhizomes of these plants in herbarium specimens and publications do not look like the Border Cave one. Orchids such as *Bulbophyllum* Thouars spp. have druses as well as raphides, thereby excluding them (53). Aponogetonaceae are inappropriate matches because they are water plants with aerenchyma which is lacking in the Border Cave rhizomes.

Two families remain potential partners for the Border Cave rhizome morphology and anatomy: Asparagaceae (in particular, *Ledebouria* Roth spp. and *Dracaena* L. spp.), and Hypoxidaceae (in particular, *Hypoxis* L. spp.). *Dracaena hyacinthoides* (L.) Mabb. occurs in the Lebombo Mountains, often in large colonies (52). Fibre from the leaves can be used to make twine, but the rhizome is not eaten by humans. *Dracaena* spp. have ring markings on their underground stems, but the rhizomes have secondary thickening meristems (54) that are lacking from the Border Cave rhizomes, so they can be eliminated. Also, in the Asparagaceae family, *Asparagus* Tourn. ex L. spp. have elongated tubers pinched at both ends and they can be disregarded on morphological grounds for they are quite different in appearance from the sub-globose Border Cave rhizome. *Ledebouria* spp., some of which are edible and grow in gregarious clumps, are suitable for harvesting as food. *Ledebouria revoluta* (L.f) Jessop is eaten, but the bulb is much larger than the Border Cave rhizome, which in any event is not a bulb because it lacks a stem covered by enlarged and fleshy leaf bases. Of all the plants examined here, Hypoxidaceae is the only family not yet eliminated. The hypothesis is therefore that the Border Cave rhizome is a member of this family. Hypoxidaceae are now examined in more detail.

Hypoxidaceae morphology and anatomy and comparison with the Border Cave rhizomes

Hypoxidaceae R.Br. is a large family with six genera in South Africa (52). *Hypoxis* spp. include three highly desirable, edible species that grow near the site: *H. angustifolia* Lam., *H. argentea* Harv. ex Baker and *H. filiformis* Baker. These small plants have white flesh and mucilage that renders their rhizomes more palatable than species with bitter, orange mucilage (for example, *H. hemerocallidea*). Large quantities of starch are contained within the fresh rhizomes (Fig. 4E), but once the specimens are charred, starch grains disappear and cannot be used for identification.

Hypoxis spp. have two types of underground stem. A few species propagate through horizontal shoots. In *Hypoxis angustifolia*, lateral buds develop into rhizome-like portions at the end of which a ‘corm’ develops (29). Many rhizomes and shoots can then develop from one plant (29) and a gregarious clump forms. This type of plant population provides an ideal source of food for plant-gatherers. *Hypoxis angustifolia*, unlike most *Hypoxis* in the area, is evergreen and blooms for much of the year, making it highly visible. Most *Hypoxis* spp. are, in contrast, erect, vertically-developing perennial geophytes (some authors favour the word rhizome, others

use the word corm, or even tuber). As Hypoxidaceae rootstocks enlarge vertically, the old bases shrink, but remain attached to the functional rhizome (29, 40, 55), sometimes as a disc of decaying tissue (31). It is feasible that plant collectors bringing geophytes to the home base for sharing and/or cooking would put the entire vegetable in the ashes to cook, but would later discard the decayed, burned basal disc. The senescent part of the organ retains little evidence of vascular structures, though root traces remain visible (55). New growth forms annually at the apex of the rhizome and the expanding part of the organ is where vasculature is concentrated (56,57). This observation was confirmed by microscopy and SEM studies of specimens of *H. argentea*, *H. angustifolia*, *H. hemerocallidea*, *H. obtusa* Burch. ex Ker Gawl., and *H. rigidula* Baker (fig. S2). Roots from the rhizome sometime grow through the decaying disc at its base (31) and this is evident in the modern vouchers. The modern *Hypoxis* roots (fig. S3A and C) closely match those in the Border Cave rhizomes. Xylem and xylem tissue are prominent in the ancient and modern roots and both are encased in fibre sheaths (rhizodermis) (Fig. 3A and B, fig. S3B, C and D). Also present in all modern *Hypoxis* specimens, are idioblasts with raphide bundles and, as in the archaeological specimens, most raphides are in the cortex.

Modern *Hypoxis* parenchyma resembles that from the Border Cave rhizomes; the cells vary in shape from angular to oval and the largest cells are about 60 µm in length. *Hypoxis* spp. vasculature is not typical of most monocotyledons, which tend to have vascular bundles scattered in the stems. Instead, the active, current portion of the *Hypoxis* rhizome has vascular bundles that lie in a ring (29) (fig. S2D). The inner ground tissue of the young *Hypoxis hemerocallidea* rhizome has amphivasal vascular bundles (57), but no such bundles were observed in the mature *Hypoxis* vouchers examined here. Rudall (39) makes the point that in some rhizomes, vascular bundles merge so that individual ones are ill-defined. This is the case in *Hypoxis* Voucher #27 which displays a large number of xylem vessels (it is not possible to count them because of the reflective surface of the burned rhizome) in a ring close to where an indistinct endodermis lies (Fig. 3C, fig. S2). Elsewhere in the same specimen, there is a possible closed collateral vascular bundle with an oval arrangement of xylem vessels, and adjacent carbonised mass of phloem (fig. S3E).

Cheadle (58) recorded ‘primitive vessels’ with scalariform perforation plates in the roots of Hypoxidaceae. A scalariform perforation plate is present at the end of a xylem tube in Voucher #27 and a scalariform sieve plate from a Border Cave rhizome root is not dissimilar.

In summary, the Border Cave rhizomes have both morphological and anatomical features in common with *Hypoxis* spp., especially *Hypoxis angustifolia*. The morphological features include the shape of the rhizome, a depressed centre on its upper (proximal) surface, radial rhexigeny, raised ring scars on the circumference and root traces that emerge from the cortex of both modern and ancient specimens, and originate within the inner ground tissue, inside of the endodermis and almost certainly within the pericycle (which is not distinguishable in the rhizomes after charring). Bundles of needle-like raphides are especially frequent in the cortex of our modern *Hypoxis* vouchers and the Border Cave specimens. The vascular structures are similar in having roots or root traces encased in fibre sheaths, parenchyma of similar size and shape, vascular bundles with twelve to sixteen (or more) xylem vessels in elongated, merged clusters, with the xylem vessels containing thickened walls of scalariform tissue.

Acknowledgements

We are especially grateful to L. Kubiak-Martens for setting us on the path of geophyte identification and for correcting our early mistakes. The collection of modern geophytes took

four years during which time many people helped with the task. We cannot mention them all by name, but we single out Bawinile Olga Vilane for accompanying us on some collecting trips in Nkungwini in 2015-2018 and for alerting us to markets where herbalists sell geophytes. Hugh and Rene Glen helped with identifications and vouchers in 2018. We used the Phenom SEM in the Evolutionary Studies Institute and we thank Kudakwashe Jakarta for guidance.



Fig. S1.

Location of Border Cave in South Africa

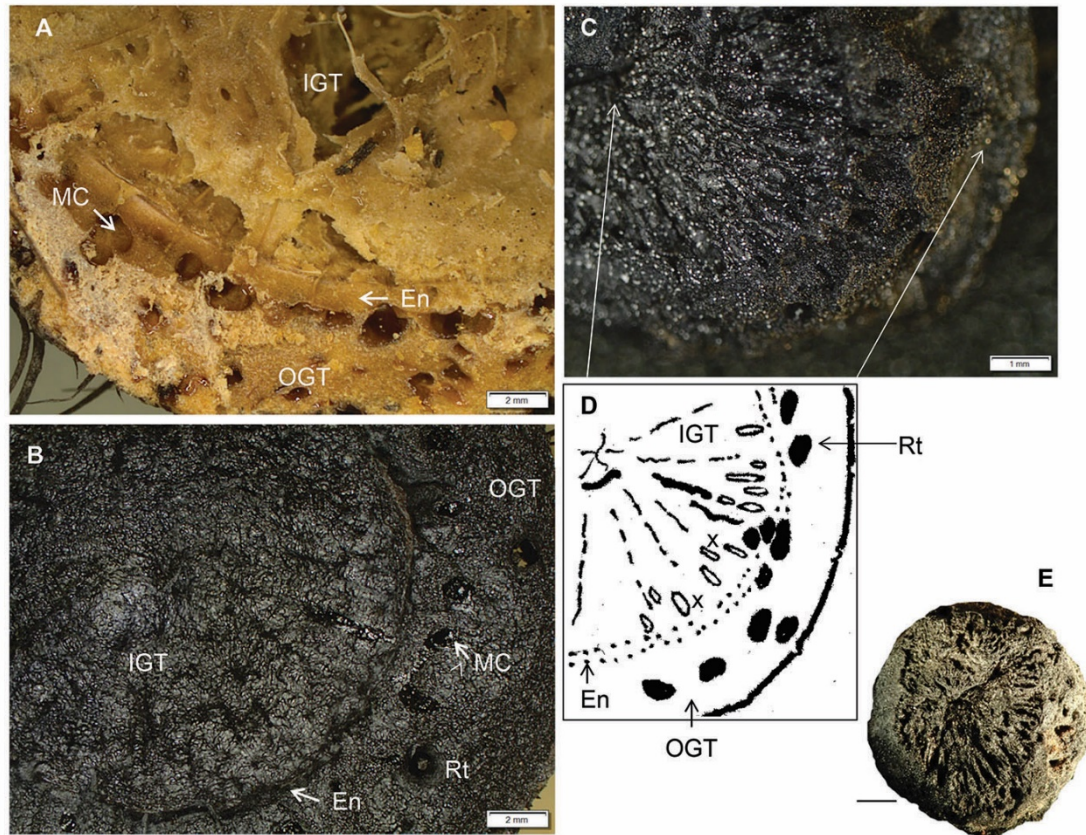


Fig. S2.

***Hypoxis* rhizome anatomy compared with that of Border Cave rhizome BC17.** (A) Fresh *Hypoxis* rhizome Voucher #62 showing inner and outer ground tissue, separated by the endodermis. Mucilage cavities are common outside the endodermis. TS; scale bar 2 mm. (B) Charred *Hypoxis* rhizome Voucher #27 showing inner and outer ground tissue, separated by the endodermis. Mucilage cavities and root traces are common outside the endodermis. TS; scale bar 2 mm. (C) One quadrant of Border Cave rhizome BC17 (see Fig. 2 and (E) for whole rhizome). The charred rhizome surface is deteriorated, but has not been cut in order to preserve it. TS; scale bar 1 mm. (D) TS sketch (not all features are to scale) of the features visible in (C) under the microscope and SEM. The inner ground tissue has radial splits and inside the endodermis is an irregular ring of xylem (x) vessel clusters (their size is exaggerated to show their distribution). Most of the root traces are outside the endodermis. (E) Border Cave rhizome BC17, upper (proximal) surface. Scale bar 2 mm. En = endodermis; MC = mucilage cavity; Rt = root (and root trace); x = xylem; IGT = inner ground tissue; OGT = outer ground tissue; TS = transverse section.

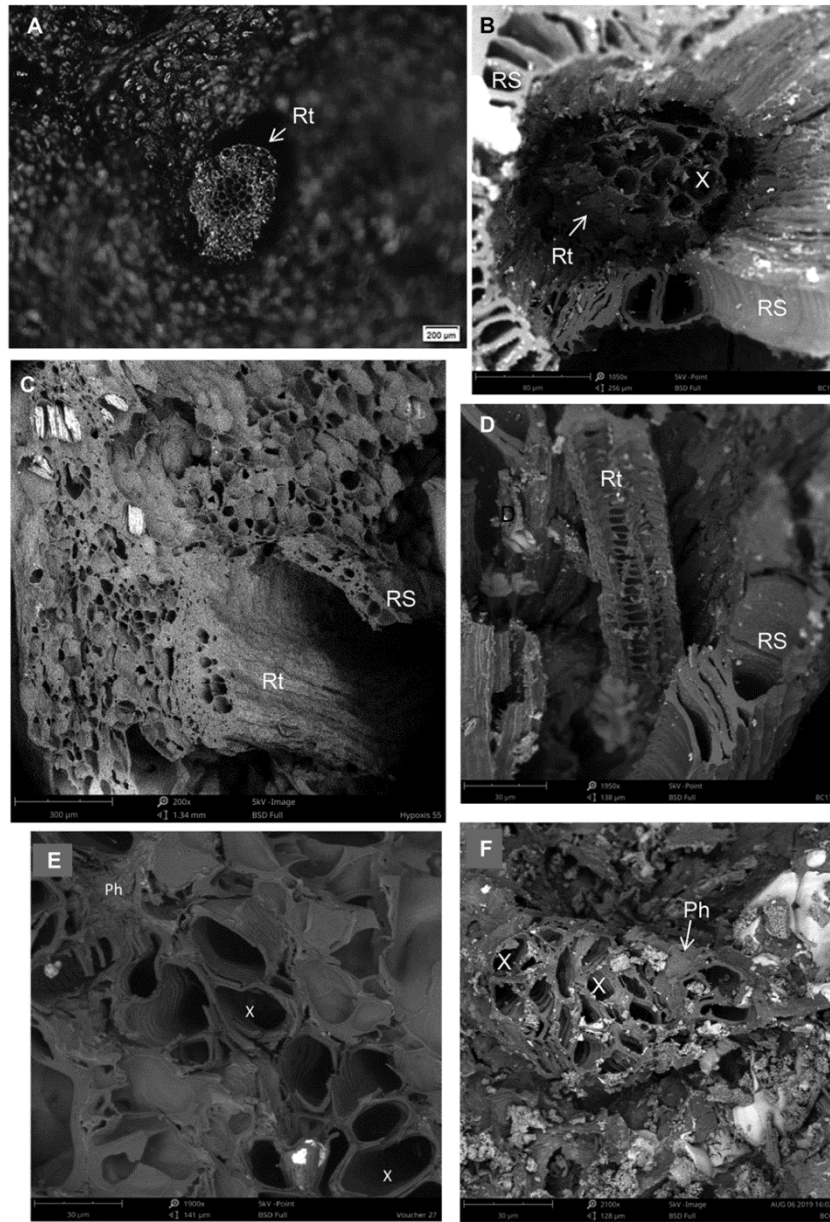


Fig. S3.

Comparison of modern *Hypoxis* charred rhizome roots and vascular bundles with those from Border Cave. (A) Modern charred *Hypoxis* rhizome Voucher #55 root. TS, scale bar 200 µm (B) Border Cave rhizome BC 17 with xylem vessels in root enclosed by rhizodermis. TS, scale bar 80 µm. (C) Modern charred *Hypoxis* rhizome Voucher #55: root with xylem vessels and rhizodermal sheath. TS, scale bar 300 µm. (D) Border Cave rhizome BC 17 with rhizodermis and broken root with longitudinally split xylem vessel showing scalariform tissue. TS, scale bar 30 µm. (E) Modern charred *Hypoxis* rhizome Voucher #27, with possible closed collateral bundle. The xylem is clearly visible, but the putative phloem is solidified carbon. TS, scale bar 30 µm. (F) Border Cave rhizome BC 6, with possible closed collateral bundle. The xylem is clearly visible, but the putative phloem is solidified carbon. TS, scale bar 30 µm. RS = rhizodermal sheath, Rt = root, X = xylem, Ph = phloem, TS = transverse section.

Table S1
Border Cave parenchyma fragments > 2 mm

Member	Layer	Frequency of parenchyma fragments > 2 mm
4 WA	Top and Pinkish Grey	1
	White 1, 2 and 3	9
	White 4, 5 and 6	5
	White 7 - 10	5
	Dark Brown layers	4
5 BS	Very Dark Greyish Brown	6
TOTAL frequency of parenchyma fragments > 2 mm		30

Table S2.

Some attributes of modern monocotyledons (36, 43, 47, 48, 59) compared with those of the Border Cave rhizome. Key: absence of data = ?; occasionally present = Oc; scalariform = scal; reticular = retic; pitted = pit; simple = simp. See text for a discussion of attributes that eliminate some of the taxa listed in the table as potential matches for the Border Cave rhizome.

FAMILY (some genera and species listed)	vessel wall thickening	root vessels	raphides present	styloids present	druses present	central corm depression	potential match for Border Cave
AMARYLLIDACEAE	?	scal	yes	no	Oc	yes	NO
<i>Tulbaghia</i> spp.	retic/scal	simp/scal	no	no	-	yes	NO
APONOGETONACEAE	?	no	?	?	?	yes	?
ARACEAE	?	scal	yes	?	?	yes	?
<i>Zantedeschia</i> spp.	?	scal	yes	no	Oc	yes	NO
ASPARAGACEAE	?	simp/scal	yes	?	?	yes	YES
<i>Chlorophytum comosum</i>	pitted	simp	no	yes	yes	yes	NO
<i>Dracaena</i> spp.	scal	simp	yes	?	?	yes	YES
<i>Ledebouria</i> spp.	retic/scal	simp/scal	yes	?	?	yes	YES
<i>Ornithogalum</i> spp.	retic/scal	simp/scal	yes	?	?	yes	YES
ASPHODELACEAE	?	simp/scal	yes	yes	?	yes	NO
<i>Aloe</i> spp.	scal	simp/scal	yes	yes	?	yes	NO
COMMELINACEAE	spiral	simp	yes	?	?	yes	NO
CYPERACEAE	?	simp	no	no	no	yes	NO
DIOSCOREACEAE	?	scal	yes	?	?	yes	YES
HYPOXIDACEAE	scal	scal	yes	no	?	yes	YES
IRIDACEAE	?	simp/scal	no	yes	no	no	NO
ORCHIDACEAE	scal	simp/?	yes	no	yes	yes	NO
TYPHACEAE	?	scal	yes	?	?	yes	YES
BORDER CAVE (BC) RHIZOME	scal	scal	yes	no	no	yes	

References and Notes

1. G. B. Silberbauer, *Hunter and Habitat in the Central Kalahari Desert* (Cambridge Univ. Press, 1981).
2. P. J. Butterworth, P. R. Ellis, M. Wollstonecroft, “Why protein is not enough: The roles of plants and plant processing in delivering the dietary requirements of modern and early *Homo*” in *Wild Harvest: Plants in the Hominin and Pre-agrarian Human Worlds*, K. Hardy, L. Kubiak-Martens, Eds. (Oxbow, Oxford, 2016), pp. 31–54.
3. J. D. Speth, K. A. Spielmann, Energy source, protein metabolism, and hunter-gatherer subsistence strategies. *J. Anthropol. Archaeol.* **2**, 1–31 (1983). [doi:10.1016/0278-4165\(83\)90006-5](https://doi.org/10.1016/0278-4165(83)90006-5)
4. E. Singels, A. J. Potts, R. M. Cowling, C. W. Marean, J. De Vynck, K. J. Esler, Foraging potential of underground storage organ plants in the southern Cape, South Africa. *J. Hum. Evol.* **101**, 79–89 (2016). [doi:10.1016/j.jhevol.2016.09.008](https://doi.org/10.1016/j.jhevol.2016.09.008) [Medline](#)
5. N. J. Dominy, E. R. Vogel, J. D. Yeakel, P. Constantino, P. W. Lucas, Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evol. Biol.* **35**, 159–175 (2008). [doi:10.1007/s11692-008-9026-7](https://doi.org/10.1007/s11692-008-9026-7)
6. R. Wrangham, Control of fire in the Palaeolithic: Evaluating the cooking hypothesis. *Curr. Anthropol.* **58** (S16), S303–S313 (2017). [doi:10.1086/692113](https://doi.org/10.1086/692113)
7. L. Wandsnider, The roasted and the boiled: Food composition and heat treatment with special emphasis on pit-hearth cooking. *J. Anthropol. Archaeol.* **16**, 1–48 (1997). [doi:10.1006/jaar.1997.0303](https://doi.org/10.1006/jaar.1997.0303)
8. M. M. Wollstonecroft, P. R. Ellis, G. C. Hillman, D. Q. Fuller, Advances in plant food processing in the Near Eastern Epipalaeolithic and implications for improved edibility and nutrient bioaccessibility: An experimental assessment of *Bolboschoenus maritimus* (L.) Palla (sea club-rush). *Veg. Hist. Archaeobot.* **17**, 19–27 (2008). [doi:10.1007/s00334-008-0162-x](https://doi.org/10.1007/s00334-008-0162-x)
9. M. Sponheimer, J. A. Lee-Thorp, Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Science* **283**, 368–370 (1999). [doi:10.1126/science.283.5400.368](https://doi.org/10.1126/science.283.5400.368) [Medline](#)
10. C. R. Peters, J. C. Vogel, Africa’s wild C4 plant foods and possible early hominid diets. *J. Hum. Evol.* **48**, 219–236 (2005). [doi:10.1016/j.jhevol.2004.11.003](https://doi.org/10.1016/j.jhevol.2004.11.003) [Medline](#)
11. J. Lee-Thorp, A. Likies, H. T. Mackaye, P. Vignaud, M. Sponheimer, M. Brunet, Isotopic evidence for an early shift to C4 resources by Pliocene hominins in Chad. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 20369–20372 (2012). [doi:10.1073/pnas.1204209109](https://doi.org/10.1073/pnas.1204209109) [Medline](#)
12. K. Hardy, J. Brand-Miller, K. D. Brown, M. G. Thomas, L. Copeland, The importance of dietary carbohydrate in human evolution. *Q. Rev. Biol.* **90**, 251–268 (2015). [doi:10.1086/682587](https://doi.org/10.1086/682587) [Medline](#)
13. A. G. Henry, A. S. Brooks, D. R. Piperno, Plant foods and the dietary ecology of Neanderthals and early modern humans. *J. Hum. Evol.* **69**, 44–54 (2014). [doi:10.1016/j.jhevol.2013.12.014](https://doi.org/10.1016/j.jhevol.2013.12.014) [Medline](#)

14. L. S. Weyrich, S. Duchene, J. Soubrier, L. Arriola, B. Llamas, J. Breen, A. G. Morris, K. W. Alt, D. Caramelli, V. Dresely, M. Farrell, A. G. Farrer, M. Francken, N. Gully, W. Haak, K. Hardy, K. Harvati, P. Held, E. C. Holmes, J. Kaidonis, C. Lalueza-Fox, M. de la Rasilla, A. Rosas, P. Semal, A. Soltysiak, G. Townsend, D. Usai, J. Wahl, D. H. Huson, K. Dobney, A. Cooper, Neanderthal behaviour, diet, and disease inferred from ancient DNA in dental calculus. *Nature* **544**, 357–361 (2017). [doi:10.1038/nature21674](https://doi.org/10.1038/nature21674) [Medline](#)
15. Y. Melamed, M. E. Kislev, E. Geffen, S. Lev-Yadun, N. Goren-Inbar, The plant component of an Acheulian diet at Gesher Benot Ya'aqov, Israel. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 14674–14679 (2016). [doi:10.1073/pnas.1607872113](https://doi.org/10.1073/pnas.1607872113) [Medline](#)
16. C. Larbey, S. M. Mentzer, B. Ligouis, S. Wurz, M. K. Jones, Cooked starchy food in hearths ca. 120 kya and 65 kya (MIS 5e and MIS 4) from Klasies River Cave, South Africa. *J. Hum. Evol.* **131**, 210–227 (2019). [doi:10.1016/j.jhevol.2019.03.015](https://doi.org/10.1016/j.jhevol.2019.03.015) [Medline](#)
17. L. Wadley, *Hunters and Gatherers of the Later Stone Age, Southern Transvaal* (Cambridge Monographs in African Archaeology 25, Oxford, 1987).
18. H. J. Deacon, *Where Hunters Gathered* (South African Archaeological Society Monograph Series 1, 1976).
19. Materials and methods are available as supplementary materials.
20. L. R. Backwell, F. d'Errico, W. E. Banks, P. de la Peña, C. Sievers, D. Stratford, S. J. Lennox, M. Wojcieszak, E. M. Bordy, J. Bradfield, L. Wadley, New excavations at Border Cave, KwaZulu-Natal, South Africa. *J. Field Archaeol.* **43**, 417–436 (2018). [doi:10.1080/00934690.2018.1504544](https://doi.org/10.1080/00934690.2018.1504544)
21. P. B. Beaumont, “Border Cave,” thesis, University of Cape Town, South Africa (1978).
22. F. d'Errico, L. Backwell, P. Villa, I. Degano, J. J. Lucejko, M. K. Bamford, T. F. G. Higham, M. P. Colombini, P. B. Beaumont, Early evidence of San material culture represented by organic artifacts from Border Cave, South Africa. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 13214–13219 (2012). [doi:10.1073/pnas.1204213109](https://doi.org/10.1073/pnas.1204213109) [Medline](#)
23. L. González Carretero, M. Wollstonecroft, D. Q. Fuller, A methodological approach to the study of archaeological cereal meals: A case study at Çatalhöyük East (Turkey). *Veg. Hist. Archaeobot.* **26**, 415–432 (2017). [doi:10.1007/s00334-017-0602-6](https://doi.org/10.1007/s00334-017-0602-6) [Medline](#)
24. C. E. Inchley, C. D. A. Larbey, N. A. A. Shwan, L. Pagani, L. Saag, T. Antão, G. Jacobs, G. Hudjashov, E. Metspalu, M. Mitt, C. A. Eichstaedt, B. Malyarchuk, M. Derenko, J. Wee, S. Abdullah, F.-X. Ricaut, M. Mormina, R. Mägi, R. Villems, M. Metspalu, M. K. Jones, J. A. L. Armour, T. Kivisild, Selective sweep on human amylase genes postdates the split with Neanderthals. *Sci. Rep.* **6**, 37198 (2016). [doi:10.1038/srep37198](https://doi.org/10.1038/srep37198) [Medline](#)
25. G. Hillman, M. Wollstonecroft, “Dietary diversity: Our species specific dietary adaptation” in *Archaeology of African Plant Use*, C. J. Stephens, S. Nixon, M. A. Murray, D. Q. Fuller, Eds. (Left Coast Press, Walnut Creek, 2014), pp. 37–49.
26. R. Grün, P. Beaumont, P. V. Tobias, S. Eggins, On the age of Border Cave 5 human mandible. *J. Hum. Evol.* **45**, 155–167 (2003). [doi:10.1016/S0047-2484\(03\)00102-7](https://doi.org/10.1016/S0047-2484(03)00102-7) [Medline](#)

27. A. R. Millard, Bayesian analysis of ESR dates, with application to Border Cave. *Quat. Geochronol.* **1**, 159–166 (2006). [doi:10.1016/j.quageo.2006.03.002](https://doi.org/10.1016/j.quageo.2006.03.002)
28. J. Wiland-Szymańska, Z. Adamski, J. Wiland-Szymanska, Taxonomic and morphological notes on *Hypoxis angustifolia* (Hypoxidaceae) from Africa, Madagascar, and Mauritius. *Novon* **12**, 142–151 (2002). [doi:10.2307/3393254](https://doi.org/10.2307/3393254)
29. Y. Singh, “Systematics of *Hypoxis* (Hypoxidaceae) in Southern Africa,” thesis, University of Pretoria, South Africa (2000).
30. J. W. Bews, J. E. Vanderplank, Storage and other carbohydrates in a Natal succulent and a Natal geophyte and their behaviour before, during, and after the winter resting season. *Ann. Bot.* **os-44**, 689–719 (1930). [doi:10.1093/oxfordjournals.aob.a090243](https://doi.org/10.1093/oxfordjournals.aob.a090243)
31. J. Wiland-Szymańska, Variability, taxonomy and phylogeny: The genus *Hypoxis* L. (Hypoxidaceae) in the East Tropical Africa: variability, distribution and conservation status. *Biodivers. Res. Conserv.* **14**, 1–129 (2009).
32. M. Jones, “Moving north: Archaeobotanical evidence for plant diet in Middle and Upper Paleolithic Europe” in *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*, J.-J. Hublin, M. P. Richards, Eds. (Springer, 2009), pp. 171–180.
33. A. S. Brooks, J. E. Yellen, R. Potts, A. K. Behrensmeyer, A. L. Deino, D. E. Leslie, S. H. Ambrose, J. R. Ferguson, F. d’Errico, A. M. Zipkin, S. Whittaker, J. Post, E. G. Veatch, K. Foecke, J. B. Clark, Long-distance stone transport and pigment use in the earliest Middle Stone Age. *Science* **360**, 90–94 (2018). [doi:10.1126/science.aao2646](https://doi.org/10.1126/science.aao2646) [Medline](#)
34. International Plant Names Index (Kewscience, 2019); <https://www.ipni.org>
35. World Checklist of Selected Plant Families (Kewscience, Royal Botanic Gardens, Kew, 2019); wcp.science.kew.org/home.do
36. R. M. T. Dahlgren, H. T. Clifford, *The Monocotyledons: A Comparative Study* (Academic Press, 1982).
37. P. H. Raven, R. F. Evert, S. E. Eichhorn, *Biology of Plants* (Worth, New York, ed. 4, 1986).
38. J. G. Hather, *Archaeological Parenchyma* (Archetype, London, 2000).
39. P. J. Rudall, Taxonomic and evolutionary implications of rhizome structure and secondary thickening in Iridaceae. *Bot. Gaz.* **145**, 524–534 (1984). [doi:10.1086/337488](https://doi.org/10.1086/337488)
40. N. L. de Menezes, P. M. Elbl, G. Cury, B. Appezzato-da-Glória, K. L. M. Sasaki, C. G. da Silva, G. R. Costa, V. G. A. Lima, The meristematic activity of the endodermis and the pericycle and its role in the primary thickening of stems in monocotyledonous plants. *Plant Ecol. Divers.* **5**, 153–165 (2012). [doi:10.1080/17550874.2011.604925](https://doi.org/10.1080/17550874.2011.604925)
41. E. Cholewa, M. Griffith, The unusual vascular structure of the corm of *Eriophorum vaginatum*: Implications for efficient retranslocation of nutrients. *J. Exp. Bot.* **55**, 731–741 (2004). [doi:10.1093/jxb/erh054](https://doi.org/10.1093/jxb/erh054) [Medline](#)
42. J. G. Hather, *An Archaeobotanical Guide to Root and Tuber Identification* (Oxbow Monograph 28, Oxford, 1993).

43. F. Kauff, P. J. Rudall, J. G. Conran, Systematic root anatomy of Asparagales and other monocotyledons. *Plant Syst. Evol.* **223**, 139–154 (2000). [doi:10.1007/BF00985275](https://doi.org/10.1007/BF00985275)
44. A. Crowther, “Re-viewing raphides: Issues with the identification and interpretation of calcium oxalate crystals in microfossil assemblages” in *New Directions in Archaeological Science*, A. Fairbairn, S. O’Connor, B. Marwick, Eds. (ANU Press, Australia, 2009), pp. 105–118.
45. J. G. Hather, The identification of charred archaeological remains of vegetative parenchymous tissue. *J. Archaeol. Sci.* **18**, 661–675 (1991). [doi:10.1016/0305-4403\(91\)90028-N](https://doi.org/10.1016/0305-4403(91)90028-N)
46. M. A. Webb, Cell-mediated crystallization of calcium oxalate in plants. *Plant Cell* **11**, 751–761 (1999). [doi:10.1105/tpc.11.4.751](https://doi.org/10.1105/tpc.11.4.751) [Medline](#)
47. C. J. Prychid, P. J. Rudall, Calcium oxalate crystals in monocotyledons: A review of their structure and systematics. *Ann. Bot.* **84**, 725–739 (1999). [doi:10.1006/anbo.1999.0975](https://doi.org/10.1006/anbo.1999.0975)
48. C. J. Prychid, R. S. Jabaily, P. J. Rudall, Cellular ultrastructure and crystal development in *Amorphophallus* (Araceae). *Ann. Bot.* **101**, 983–995 (2008). [doi:10.1093/aob/mcn022](https://doi.org/10.1093/aob/mcn022) [Medline](#)
49. A. C. Rodrigues, M. E. M. Estelita, Morphoanatomy of the stem in Cyperaceae. *Acta Bot. Bras.* **23**, 889–901 (2009). [doi:10.1590/S0102-33062009000300030](https://doi.org/10.1590/S0102-33062009000300030)
50. C. J. Prychid, C. A. Furness, P. J. Rudall, Systematic significance of cell inclusions in Haemodoraceae and allied families: Silica bodies and tapetal raphides. *Ann. Bot.* **92**, 571–580 (2003). [doi:10.1093/aob/mcg172](https://doi.org/10.1093/aob/mcg172) [Medline](#)
51. C. Ekeke, J. U. Agogbua, Anatomical study on *Commelina diffusa* Burn f. and *Commelina erecta* L. (Commelinaceae). *J. Appl. Sci. Environ. Manag.* **22**, 7–11 (2018). [doi:10.4314/jasem.v22i1.2](https://doi.org/10.4314/jasem.v22i1.2)
52. E. Pooley, *A Field Guide to Wild Flowers of KwaZulu-Natal and the Eastern Region* (Flora Publications Trust, Durban, Natal, 1998).
53. T. Muthukumar, M. Shenbagam, Vegetative anatomy of the orchid *Bulbophyllum sterile* (Orchidaceae: Epidendroideae). *Lankesteriana* **18**, 13–22 (2009).
54. P. J. Rudall, New records of secondary thickening in monocotyledons. *IAWA J.* **16**, 261–268 (1995). [doi:10.1163/22941932-90001409](https://doi.org/10.1163/22941932-90001409)
55. M. F. Thompson, Studies in the Hypoxidaceae. I. Vegetative morphology and anatomy. *Bothalia* **12**, 111–117 (1976). [doi:10.4102/abc.v12i1.1383](https://doi.org/10.4102/abc.v12i1.1383)
56. S. L. Munro, “A morphological-anatomical classification of growth forms in monocotyledons,” thesis, University of Cape Town, South Africa (2000).
57. A. D. Bayley, “The biosynthesis and production of hypoxoside in *Hypoxis hemerocallidea* Fisch. and Mey. in vivo and in vitro,” thesis, University of Natal, Pietermaritzburg, South Africa (1989).
58. V. I. Cheadle, Vessels in Haemodoraes. *Phytomorphology* **18**, 413–420 (1968).

59. P. J. Rudall, Anatomy and systematics of Iridaceae. *Bot. J. Linn. Soc.* **114**, 1–21 (1994).
[doi:10.1111/j.1095-8339.1994.tb01920.x](https://doi.org/10.1111/j.1095-8339.1994.tb01920.x)