ARCHAEOLOGY

Cooked starchy rhizomes in Africa 170 thousand years ago

Lyn Wadley[1]*, Lucinda Backwell[1,2], Francesco d'Errico[3,4], Christine Sievers[5]

Plant carbohydrates were undoubtedly consumed in antiquity, yet starchy geophytes were seldom preserved archaeologically. We report evidence for geophyte exploitation by early humans from at least 170,000 years ago. Charred rhizomes from Border Cave, South Africa, were identified to the genus *Hypoxis* L. by comparing the morphology and anatomy of ancient and modern rhizomes. *Hypoxis angustifolia* Lam., the likely taxon, proliferates in relatively well-watered areas of sub-Saharan Africa and in Yemen, Arabia. In those areas and possibly farther north during moist periods, *Hypoxis* rhizomes would have provided reliable and familiar carbohydrate sources for mobile groups.

Ancient hunting strategies receive more attention from archaeologists than plant collecting, because plant preservation is often poor in archaeological sites. A plant diet, though sometimes invisible, must have contributed substantially to food security in the past, as reported for hunter-gatherers in Africa during the last century (*1*). African venison is especially lean in the dry season; thus, human populations able to supplement meat diets with carbohydrate or fat avoided malnourishment (*2*, *3*). Geophytes (corms, bulbs, tubers, and rhizomes) store starch in their underground organs, and these underground portions become sources of carbohydrate for humans and those animals able to excavate them. Modern collecting of edible geophytes in South Africa demonstrates that a gatherer's daily caloric requirement can be met within 2 hours (*4*), and such foods may become dietary staples. Cooking increases digestibility of meat and plant food, reduces toxicity, and, in the case of geophytes, has a considerable softening effect (*5*), eases peeling and chewing, and enhances glucose availability (*6*, *7*).

Before the use of fire, hominins may have eaten geophytes raw, especially Cyperaceae and aquatic plants, though some of these first required pulverizing (*8*). No geophyte remains have been recovered from early, pre-fire sites. Instead, circumstantial evidence is from sources such as isotopes, DNA, or dental calculus (*9*–*14*). Seeds from several edible geophytes and aquatic plants were found in samples from 780 thousand years (ky) ago at Gesher Benot Ya'aqov in Israel (*15*); the samples contained seeds rather than the geophytes themselves, perhaps because no trace remains after consumption of geophytes. At Klasies River, South Africa, 120-ky-old charred parenchyma fragments from unidentified geophytes imply cooking (*16*). Holocene layers of Bushman Rock Shelter and Melkhoutboom, South Africa, yielded geophytes including *Hypoxis* spp. (*17*, *18*). Here, we present earlier evidence, from at least 170 ky ago, for the cooking of identified edible rhizomes from Border Cave, northern KwaZulu-Natal, South Africa (*19*) (fig. S1).

Border Cave formed in a Lebombo Mountain cliff facing west across eSwatini (Fig. 1A). The cave was extensively excavated from early in the 1900s (*20*), but little attention was given to its botanical remains, apart from preliminary studies of 40-ky-old seeds and leaves (*21*) and chemical identifications of plant poison and resin (*22*). The cave has alternating brown sand (BS) and white ash (WA) stratigraphic members (*21*), and rhizomes were recovered from the 5 Brown Sand (5 BS) and 4 White Ash (4 WA) samples. Discrete layers are discernible in each member (Fig. 1B). The majority of identified 4 WA rhizomes come from White 8 to 5 (Table 1), which are combustion features near the base of the member. Only humans could have transported whole rhizomes from the field to the cave. The Border Cave specimens were preserved because they were charred and presumably because they were lost while roasting in the ashes, from which they were recovered archaeologically (Fig. 2). Nothing indicates that the rhizomes were pulverized

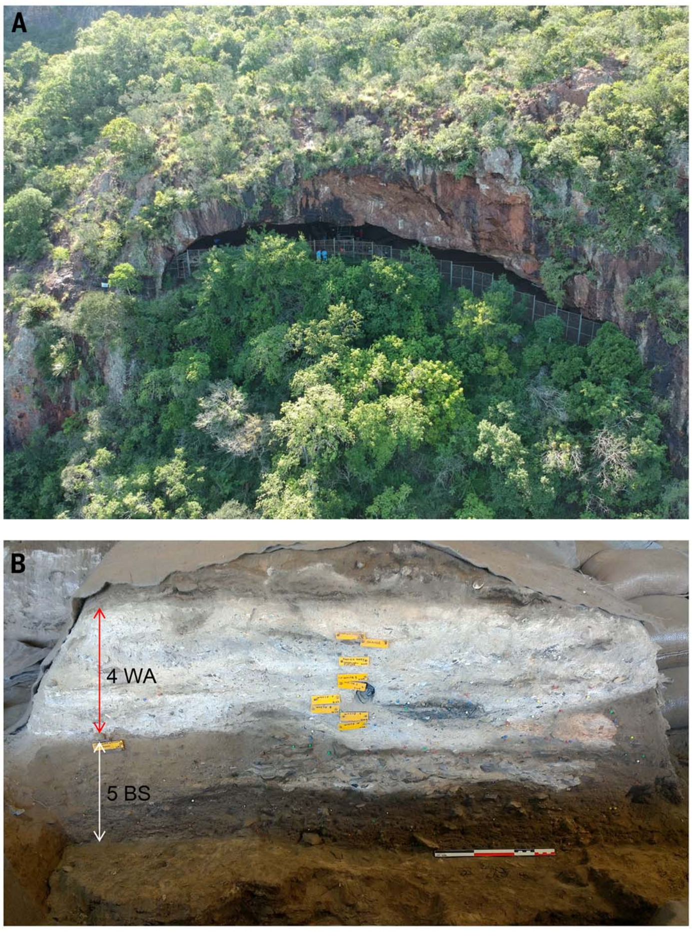

Fig. 1. Border Cave entrance and stratigraphy in Members 5 BS and 4 WA. (**A**) Border Cave perched on a cliff in the Lebombo Mountains. (**B**) Border Cave stratigraphy, excavated from 2015 to 2018, from Members 5 BS and 4 WA in Squares N108 E113 and N109 E113. Note the stacked combustion features in 4 WA. Scale bar, 30 cm.

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(*23*), but circumstantial evidence for cooking is compelling. The spatial context of the rhizomes in ash rather than adjacent sediment is significant. Further support for cooking comes from amylase gene analysis results, which indicate that a high starch diet, possibly involving processing and/or cooking of carbohydrate-rich geophytes by early humans, was already in place by the Middle Pleistocene (*24*). Cooking enables dietary diversity (*25*), and transporting geophytes to a home base like Border Cave facilitates both food processing and sharing.

The early Middle Stone Age occupations at Border Cave were dated by electron spin resonance on tooth enamel to 161 ± 10 and 144 ± 11 ky ago for 5 BS and 168 ± 5, 115 ± 8, and 113 ± 5 ky ago for 4 WA (means ± standard errors) (*26*). Bayesian analysis to obtain 95.4% probability ranges for boundaries between members indicated that Member 5 BS occupations may have commenced around 177 ky ago, while those in 4 WA began about 150 ky ago and terminated no later than 99 ky ago (*27*).

The term rhizome is used here (supplementary text), following the terminology of Wiland-Szymańska and Adamski (*28*) and Singh (*29*). The Border Cave 5 BS and 4 WA rhizomes comprise 55 complete, charred specimens (Table 1) that seem to belong to the same taxon, as well as fragments of charred parenchyma that cannot be securely identified (table S1). They are typically globose with a convex or slightly conical base, a depressed center on the proximal surface, radial splits in the ground tissue, rings from leaf scars or fiber on the outer circumference (Fig. 2), and root traces emerging from fiber sheaths within the cortex (Fig. 3B). High magnification using scanning electron microscopy (SEM) reveals distinctive anatomical features, notwithstanding the deterioration caused by charring and mechanical abrasion by cave sediment (supplementary text). Vascular bundles mostly comprise elongated clusters of xylem vessels (12 to >20) with thickened walls of scalariform tissue (Fig. 3D). Parenchyma cells, when not fused into a solid carbon mass, have geometric or oval shapes. The outer ground tissue (cortex) contains many bundles of needle-like raphides of calcium oxalate (Fig. 3F) that are also present in lower frequencies in the inner ground tissue (pith). All of these morphological and anatomical features match those of modern *Hypoxis* L. spp. rhizomes (Fig. 3, A, C, and E; figs. S2 and S3). Attributes of geophytes from other families appropriate to the area did not match the Border Cave specimens (supplementary text; table S2).

The morphology of the Border Cave rhizomes is suggestive of *Hypoxis angustifolia* Lam. (Fig. 4, A, B, and C) rather than the tiny *H. filiformis* Baker or large *H. hemerocallidea* Fisch., C.A.Mey. & Avé-Lall. The relatively small, slender-leafed *Hypoxis* taxa, such as

Table 1. Border Cave whole rhizome frequencies in Members 5 BS and 4 WA.

Member	Layer	Frequency of whole rhizomes
4 WA	Top and Pinkish Grey	6
	White 1, 2, and 3	8
	White 5 and 6	14
	White 7 and 8	13
	Reddish Brown lan, Dark Brown pit	3
5 BS	Very Dark Grey and Slump	6
	Dark Greyish Brown	5
Total		55

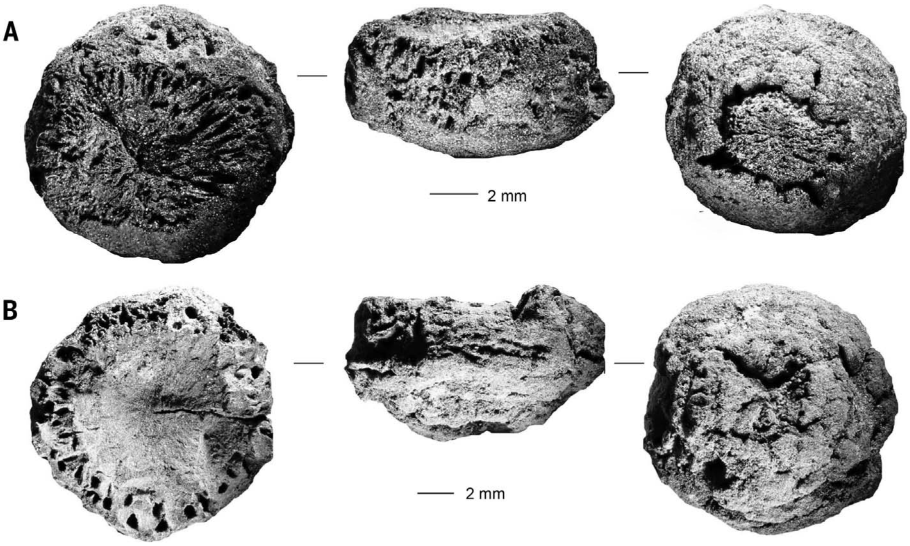

Fig. 2. Two whole Border Cave charred rhizomes. (**A**) Three views of Border Cave rhizome BC 17 from Square N108 E114, Member 4 WA, layer White 6.1 Idaho (#9577). The proximal end (top left) has been abraded, exposing radial splits caused by charring the fresh organ. Scale bar, 2 mm. (**B**) Three views of Border Cave rhizome BC 6 from Square N108 E114, Member 4 WA, layer White 6 Idaho (#9433). The rhizome proximal end (left) has a marked central depression and cavities, some of which are root cavities on the circumference. The rhizome profile (center) has a few raised ring scars, and the distal end (right) has a wrinkled, convex base. Scale bar, 2 mm.

H. angustifolia, *H. argentea* Harv. ex Baker, and *H. filiformis*, have rhizomes with white (Fig. 4) or pale yellow flesh. They are more palatable than the orange-fleshed rhizomes from plants such as *H. hemerocallidea* (*29*) and are therefore favored as food. While they are edible raw, *Hypoxis* rhizomes have high fracture toughness until they are cooked (*5*). The rhizomes are nutritious with an energy value of approximately 500 KJ/100 g, supplemented by essential vitamins and minerals (*17*). *H. hemerocallidea* rhizomes have constant carbohydrate composition year-round, though soluble sugars are slightly reduced during the resting season (*30*).

H. angustifolia, *H. argentea*, *H. filiformis*, and *H. hemerocallidea* grow in the Border Cave area, but recent overexploitation has reduced their populations. *H. angustifolia* is gregarious, propagates readily from rhizome side shoots (Fig. 4C), and retains visibility year-round, unlike deciduous *Hypoxis* species. It thrives in a variety of modern habitats and is thus likely to have had a wide distribution in the past as it does today. It occurs in sub-Saharan Africa, Sudan (to about 13°N), some Indian Ocean islands, and as far afield as Yemen (Fig. 4D) (*28*, *31*). Its modern occurrence in Yemen may indicate wider distribution of the rhizome during previous periods of humid conditions.

The Border Cave discovery is early evidence of cooked starchy plant food. The wide distribution of *Hypoxis*, particularly the small, palatable *Hypoxis angustifolia* rhizome that

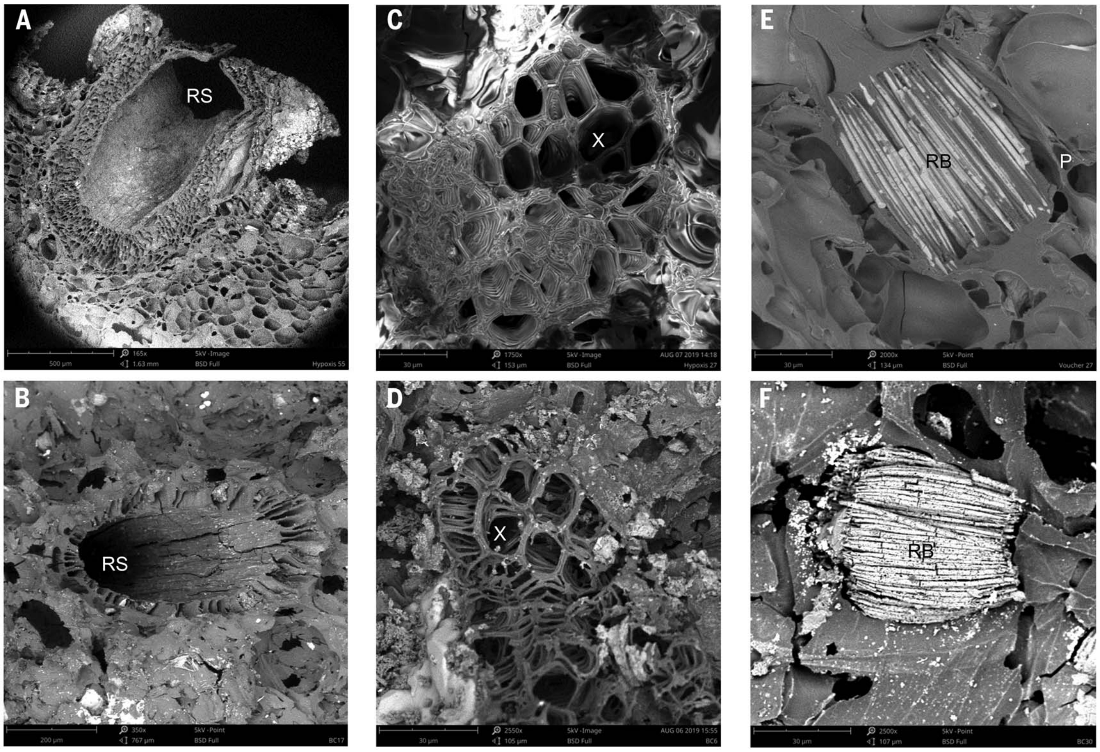

Fig. 3. Selected anatomical features of modern charred *Hypoxis* rhizomes compared with Border Cave rhizomes. (**A**) Modern charred *Hypoxis* rhizome #55 with rhizodermal sheath. Transverse section (TS) scale, 500 μm. (**B**) Border Cave rhizome BC 17 with rhizodermal sheath. TS scale, 200 μm. (**C**) Modern charred *Hypoxis* rhizome #27, cluster of xylem vessels with walls of scalariform tissue. TS scale, 30 μm. (**D**) Border Cave BC 6, cluster of xylem vessels with walls of scalariform tissue. TS scale, 30 μm. (**E**) Modern, charred *Hypoxis* rhizome #27 with raphide bundle. TS scale, 30 μm. (**F**) Border Cave rhizome BC 30, raphide bundle. TS scale, 30 μm. X, xylem; P, parenchyma; RB, raphide bundle; RS, rhizodermal sheath.

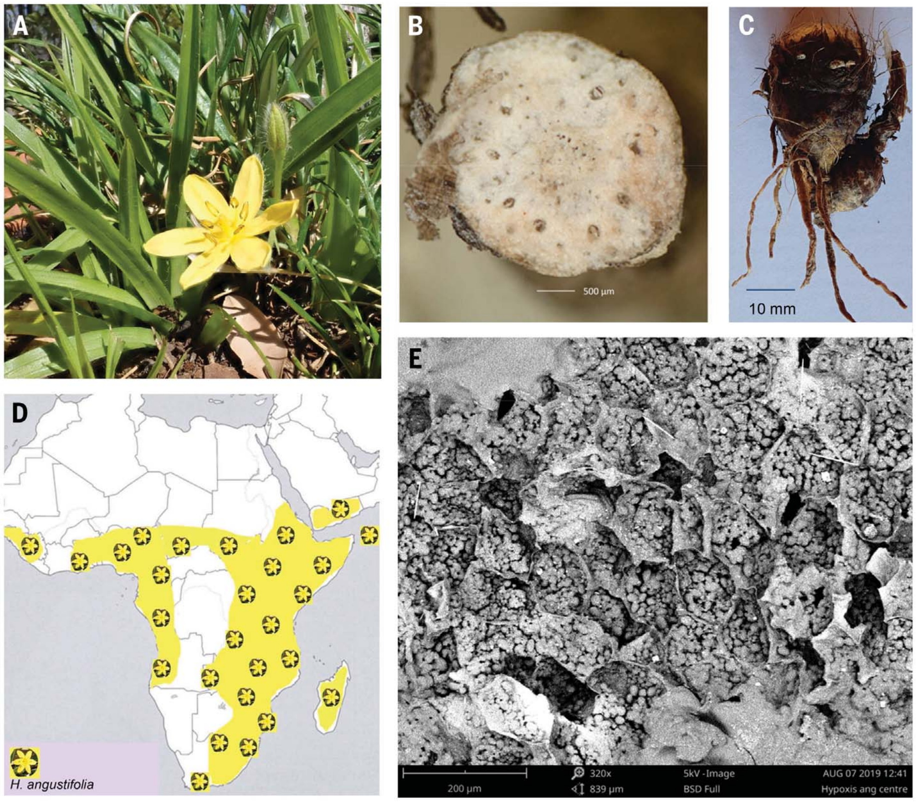

Fig. 4. Modern *Hypoxis angustifolia* field appearance, morphology, anatomy, and distribution. (**A**) *H. angustifolia* habit. (**B**) *H. angustifolia* fresh rhizome, cut transversely to reveal white flesh. Scale bar, 500 μm. (**C**) *H. angustifolia* mature fresh rhizome (left) with developing offshoot (right). Scale bar, 10 mm. (**D**) Simplified distribution of *H. angustifolia* through Africa, Yemen, and Indian Ocean islands. (**E**) *H. angustifolia* fresh rhizome cut transversely to expose parenchyma cells filled with starch grains. Scale bar, 200 μm.

grows gregariously in many habitats, implies that it could have provided a reliable, familiar staple food source for early humans moving within or out of Africa. Monocotyledons also provided food security when people moved through southern Europe during the Palaeolithic (*32*). Certain raw materials found in the Middle Stone Age site of Olorgesailie, East Africa, had distant origins by ≥295 to ~320 ky ago, implying that mobile networks were longstanding (*33*). Border Cave is remote from dispersal routes out of Africa, yet the site contributes data (*19*) for assessing the ease with which early *Homo sapiens* could travel within the continent.

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/367/6473/87/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S3
Tables S1 and S2
References (*34–59*)

View/request a protocol for this paper from *Bio-protocol*.

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Cooked starchy rhizomes in Africa 170 thousand years ago

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Middle Stone Age cooking

Early evidence of cooked starchy plant food is sparse, yet the consumption of starchy roots is likely to have been a key innovation in the human diet. Wadley *et al.* report the identification of whole, charred rhizomes of plants of the genus *Hypoxis* from Border Cave, South Africa, dated up to 170,000 years ago. These archaeobotanical remains represent the earliest direct evidence for the cooking of underground storage organs. The edible *Hypoxis* rhizomes appear to have been cooked and consumed in the cave by the Middle Stone Age humans at the site. *Hypoxis* has a wide geographical distribution, suggesting that the rhizomes could have been a ready and reliable carbohydrate source for *Homo sapiens* in Africa, perhaps facilitating the mobility of human populations.

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