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RESEARCH ARTICLE

Mechanical Properties of Plant Underground Storage Organs and Implications for Dietary Models of Early Hominins

Nathaniel J. Dominy · Erin R. Vogel · Justin D. Yeakel · Paul Constantino · Peter W. Lucas

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Abstract The diet of early human ancestors has received renewed theoretical interest since the discovery of elevated δ^{13}C values in the enamel of *Australopithecus africanus* and *Paranthropus robustus*. As a result, the hominin diet is hypothesized to have included C_4 grass or the tissues of animals which themselves consumed C_4 grass. On mechanical grounds, such a diet is incompatible with the dental morphology and dental microwear of early hominins. Most inferences, particularly for *Paranthropus*, favor a diet of hard or mechanically resistant foods. This discrepancy has invigorated the longstanding hypothesis that hominins consumed plant underground storage organs (USOs). Plant USOs are attractive candidate foods because many bulbous grasses and cormous sedges use C_4 photosynthesis. Yet mechanical data for USOs—or any putative hominin food—are scarcely known. To fill this empirical void we measured the mechanical properties of USOs from 98 plant species from across sub-Saharan Africa. We found that rhizomes were the most resistant to deformation and fracture, followed by tubers, corms, and bulbs. An important result of this study is that corms exhibited low toughness values (mean = 265.0 J m^{-2}) and relatively high Young's modulus values (mean = 4.9 MPa). This combination of properties fits many descriptions of the hominin diet as consisting of hard-brittle objects. When compared to corms, bulbs are tougher (mean = 325.0 J m^{-2}) and less stiff (mean = 2.5 MPa). Again, this combination of traits resembles dietary inferences, especially for *Australopithecus*, which is predicted to have consumed soft-tough foods. Lastly, we observed the roasting behavior of Hadza hunter-gatherers and measured the effects of roasting on the toughness on undomesticated tubers. Our results support assumptions that roasting lessens the work of mastication, and, by inference, the cost of digestion. Together these findings provide the first mechanical basis for discussing the adaptive advantages of roasting tubers and the plausibility of USOs in the diet of early hominins.

Keywords *Australopithecus* · *Paranthropus* · Diet · Hypogeous plant foods · Geophytes · Tubers · Fracture toughness · Young's modulus

Introduction

A severe drought on Daphne Major, Galápagos, in 1977 caused an 85% decline in a population of Darwin's finches, *Geospizia fortis*. The decline was correlated with a reduction in the abundance of seeds, the staple food of *G. fortis* during the dry season when insects and other plant matter are scarce. In 1977, during the normally lush wet

N. J. Dominy (✉) · E. R. Vogel
Department of Anthropology, University of California, 1156 High Street, Santa Cruz, CA 95064, USA
e-mail: njdominy@ucsc.edu

E. R. Vogel
e-mail: evogel@ucsc.edu

N. J. Dominy · J. D. Yeakel
Department of Ecology and Evolutionary Biology, University of California, 1156 High Street, Santa Cruz, CA 95064, USA
e-mail: jyeakel@pmc.ucsc.edu

P. Constantino · P. W. Lucas
Anthropology Department, The George Washington University, Hortense Amsterdam House, 2110 G Street, NW, Washington, DC 20052, USA
e-mail: pcma@gwu.edu

P. W. Lucas
e-mail: pwlucas@gwu.edu

season, larger birds fed heavily on seeds extracted from the hard mericarps of *Tribulus cistoides* (Zygophyllaceae), a food ignored by almost all birds in earlier years. Selective mortality was weakest among larger birds, and subsequent generations possessed relatively larger beaks. This episode of intense natural selection on beak morphology was a signal event in the study of evolution. The resulting publications were among the first to demonstrate that adaptive radiations could result from periods of rapid selection (Boag and Grant 1981, 1984; Schluter and Grant 1984; Grant and Grant 2002). The authors were also among the first to quantify the hardness of natural food objects.

The seeds of *Tribulus cistoides* may be classified as a fallback food, i.e., an exigent resource that *Geospizia fortis* utilized when preferred foods were scarce (Marshall and Wrangham 2007). Since the pioneering research on Daphne Major 30 years ago, authors have emphasized the vital role of fallback foods in driving adaptive radiations. For instance, Kinzey and others have stressed the importance of obdurate fruit tissues in shaping the diversity of primate communities (Rosenberger and Kinzey 1976; Terborgh 1983; Kinzey and Norconk 1990, 1993; Lambert et al. 2004). These authors argued that the partitioning of food resources on the basis of mechanical properties is expected to result in behavioral, ecological, and phenotypic adaptations. For example, hard-object feeding (durophagy) among distantly related species is linked to the parallel evolution of certain functional traits, such as robust jaws, large chewing muscles, and flat, thickly enameled molars that are pitted during life. The prominence of these same craniodental characteristics in the human clade has led to the widespread view that early hominins, *Paranthropus* in particular, chewed hard or mechanically resistant foods, perhaps during fallback episodes (Table 1).

Candidate fallback foods for early hominins include seeds and plant underground storage organs (USOs). The evidence in support of USOs is based largely on ecological, morphological, and isotopic comparisons with living USO-consumers, notably baboons, bush pigs, and mole rats (Robinson 1954; Jolly 1970; Hatley and Kappelman 1980; Peters and O'Brien 1981; Conklin-Brittain et al. 2002; Laden and Wrangham 2005; Sponheimer et al. 2005a, b; Yeakel et al. 2007). Yet the plausibility of USOs as a fallback food depends in part on their physical properties, and quantitative data from USOs—or any putative food in the hominin diet—are scarcely known (Peters and Maguire 1981; Peters 1993). To fill this empirical void we surveyed the mechanical characteristics of USOs from across sub-Saharan Africa. We

Table 1 Inferred physical characteristics of hominin diets

Species	Mechanical characteristics of the diet	Basis for inference
Ardipithecus ramidus	…less tough and abrasive than the diet of *Australopithecus*…	Comparative morphology[a]
Australopithecus afarensis	…hard foods…	Dental microwear[b]
	…harder, brittle fallback foods… (relative to early *Homo*)	Molar topography[c]
	…soft or tough foods…	Dental microwear[d]
Australopithecus africanus	…something very hard…	Comparative morphology[e]
	…a variably tougher diet than *P. robustus*…	Dental microwear[f]
Australopithecus anamensis	…hard-tough (rather than hard-brittle) foods…	Comparative morphology[g]
	…non-habitual consumption of tough foods, but a high proportion of fine abrasives rather than hard, brittle objects…	Dental microwear[h]
Paranthropus boisei	…foods that were small or hard and round in shape…	Comparative morphology[i]
	…unusually hard or tough food objects…	Masticatory biomechanics[j]
	…foods with similar ranges of toughness as those consumed by *Australopithecus africanus*, but not harder and brittler than *P. robustus*…	Dental microwear[k]
Paranthropus robustus	…small amounts of small abrasive food objects…	Model of mastication[l]
	…substantially more hard food items than *Australopithecus africanus*…	Dental microwear[m]
	…hard, brittle foods were an occasional but important part of the diet…	Dental microwear[f]
	…likely ate foods that were on average much harder and less tough than *P. boisei*…	Dental microwear[k]
Early *Homo*	…tougher, elastic fallback foods… (relative to *Australopithecus afarensis*)	Molar topography[c]
	…neither extremely hard nor exceedingly tough foods…	Dental microwear[n]
Homo erectus	… less capable of crushing hard objects but better able to shear tougher foods than *Homo rudolfensis, Homo habilis*, and earlier hominins…	Literature review[o]
'Basal hominid'	…small, solid, spherical, and hard…	Comparative ecology[p]

[a] White et al. 2006; [b] Ryan and Johanson 1989; [c] Ungar 2004; [d] Grine et al. 2006b; [e] Kay 1985; [f] Scott et al. 2005; [g] Macho et al. 2005; [h] Grine et al. 2006a; [i] Demes and Creel 1988; [j] Hylander 1988; [k] Ungar et al. 2008; [l] Lucas et al. 1985; [m] Grine and Kay 1988; [n] Ungar et al. 2006a; [o] Ungar et al. 2006b; [p] Jolly 1970

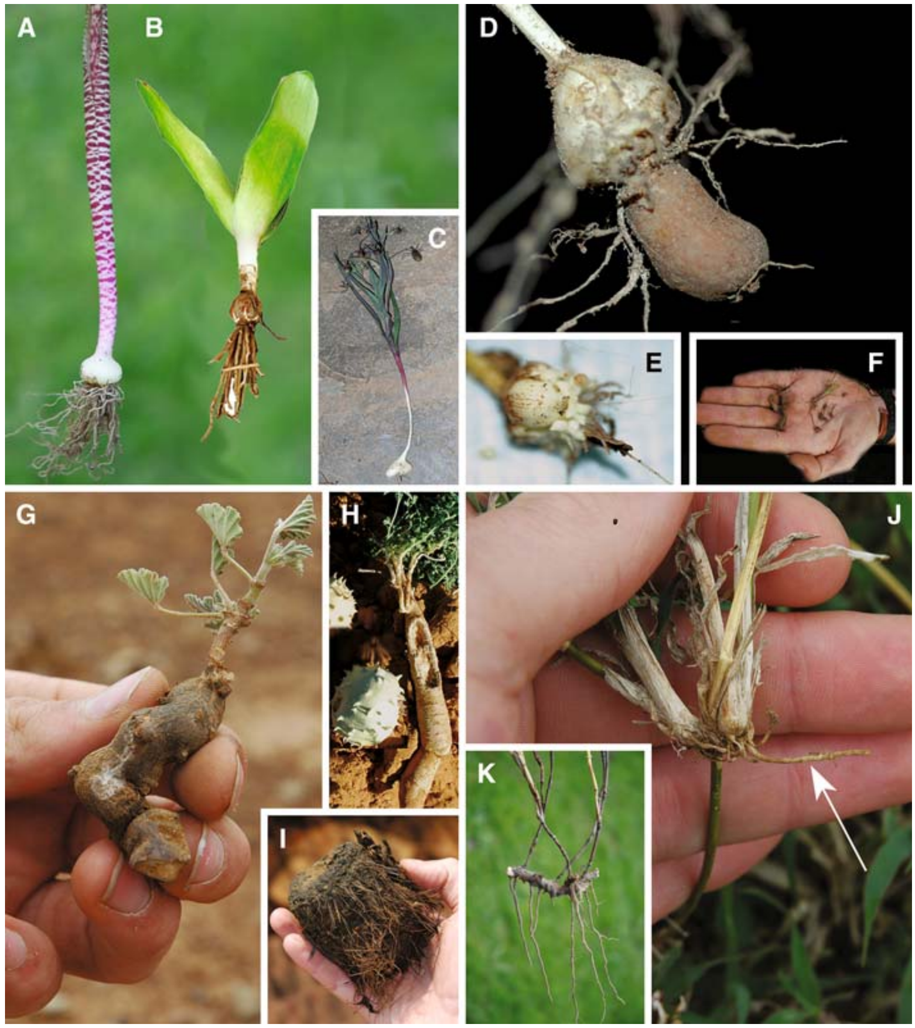

Fig. 1 The diverse morphology of plant underground storage organs. (**a**) Bulb of *Lachenalia unifolia* (Hyacinthaceae). (**b**) Bulb of *Drimia capensis* (Hyacinthaceae). (**c**) Bulb of *Ornithogalum viride* (Hyacinthaceae). (**d**) Perennating corms of *Hesperantha falcata* (Iridaceae). (**e**) Corm and cormels of *Sparaxis bulbifera* (Iridaceae). (**f**) Corms of *Cyperus cristatus* (Cyperaceae); we observed olive baboons (*Papio anubis*) peeling the tunics and consuming the parenchymatous tissue of this species. (**g**) Tuber of *Monsonia longipes* (Geraniaceae). (**h**) Tuber and fruit of *Acanthosicyos naudinianus* (Cucurbitaceae); the tuber is partially eaten by the Damaraland mole rat (*Cryptomys damarensis*). (**i**) Tuber of *Hypoxis hemerocallidea* (Hypoxidaceae). (**j**) Rhizome of *Cynodon dactylon* (Poaceae). (**k**) Rhizome of *Willdenowia incurvata* (Restionaceae)

present the data here and contextualize the concept of food hardness by comparing our results to foods in the diets of chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*). Such a comparative framework is instructive for testing evolutionary hypotheses. On the basis of dental morphology, the australopithecine diet is predicted to have been similar mechanically to the diet of orangutans and substantially harder—at least seasonally—than the diet of chimpanzees (Walker 1981; Kay 1985; Demes and Creel 1988; Vogel et al. 2008).

We also consider the effects of human processing behaviors. The importance of tubers in the diet of early *Homo* is a subject of considerable theoretical attention (O'Connell et al. 1999, 2002). For instance, Wrangham et al. suggested that the technical capacity to roast meat and tubers was a contributing factor to the emergence and spread of *Homo erectus* (Wrangham et al. 1999; Wrangham and Conklin-Brittain 2003). The authors hypothesized that roasting behavior conferred a selective advantage to early *Homo* because it softened the starchy parenchymatous tissues of tubers and improved chewing and digestive efficiency. Although corroborating archeological evidence is scant, roasting behavior may have facilitated the increased encephalization, larger body size, and reduced masticatory complex of early *Homo* (Wrangham et al. 1999). To test an underlying assumption of the hypothesis—that roasting behavior affects tuber fracture properties—we conducted a pilot field study of tubers roasted by Hadza hunter-gatherers in northern Tanzania; the results are presented here.

Methods

Classification and Collection of Plant USOs

Plant USOs are starchy geophytic structures such as bulbs, corms, rhizomes, and tubers. They function to retain water and carbohydrates during unfavorable periods for plant growth. They are commonly associated with petaloid monocots in relatively arid, Mediterranean-like ecosystems, although they are present in some dicots and habitats throughout the world. With >2,000 species, the alpha diversity of USOs is highest in South Africa. Nearly 40% of monocots in the Cape floristic region possess USOs (Procheş et al. 2006). In the Upper Karoo of South Africa, the bulb and tuber biomass of four human-edible species averages 115 MT ha^{-1} (Youngblood 2004). Specific diversity is lower in East African savannas, but the biomass of just one tuber species can exceed 50 MT ha^{-1} (Vincent 1985a).

We classified USO structures according to the definitions of Pate and Dixon (1982) or the descriptions of Manning et al. (2002). The classification of USOs frequently, though not invariably, follows taxonomic lines. Bulbs are the modified shoots of a vertically compacted stem with overlapping swollen scales (Fig. 1a–c). Corms are swollen, compacted underground stems. They are almost always vertical and never posses scales (Fig. 1d–f). Tubers are uniformly thickened perennial roots or irregular swellings on portions of the branched root system and/or adventitious roots (Fig. 1g–i). Rhizomes are horizontal underground stems that can produce roots and shoots from nodes; they are also known as rootstalks or creeping rootstalks (Fig. 1j–k).

Despite such morphological variation, the parenchymatous tissues of all USOs possess starch grains, which are a food resource for herbivores, including humans, throughout sub-Saharan Africa (Hladik et al. 1984; Malaisse and Parent 1985; Vincent 1985a; Campbell 1986; Peters 1990, 1994, 1996; Peters et al. 1992). To estimate variation in the mechanical properties of USOs, we sampled plants from diverse habitats and clades. The samples were collected with a digging stick, trowel, or shovel and the aid of local informants or staff at a variety of research facilities.

Study Locations

East Africa

In July 2005, we sampled USOs from the Mpala Research Centre, Laikipia District, Kenya (0°6′N, 37°2′E). The area is a semiarid bushland and savanna used for commercial ranching, subsistence pastoralism, tourism, and small-scale agriculture. The climate is seasonal with ca. 500 mm of rainfall year^{-1}, occurring typically in April–July and October–November. *Cyperus* corms (Cyperaceae) are a major fallback food for *Papio anubis* in Laikipia and *Papio cynocephalus* in southern Kenya (Barton 1993; Altmann 1998; Fig. 1f). Plant taxonomy follows Agnew and Agnew (1994).

We also sampled tubers from the vicinity of Lake Eyasi and the agricultural settlement of Mangola, northern Tanzania (3°25′S, 35°25′E). The habitat is savanna woodland with ca. 500 mm of rainfall year^{-1}, occurring mostly in November–April. The tubers of *Vigna* spp. (Fabaceae) in the region are a key food resource for Hadza hunter-gatherers. The Hadza subsist by gathering tubers, fruit, and honey and by hunting or scavenging medium- to large-sized game (Tomita 1966; Woodburn 1968; Vincent 1985a; O'Connell et al. 1988; Marlowe 2002). Plant taxonomy and Hadza nomenclature follows Vincent (1985b).

Southern Africa

In August 2005, we sampled USOs from the field camp of the Henry Oppenheimer Okavango Research Center, Chief's Island, Nxaraga Lagoon area, Botswana (19°24′S, 23°10′E). The area is an alluvial fan of the Okavango River; it consists of permanent and semi-permanent swamps, channels, and islands with a diversity of vegetation types (McCarthy and

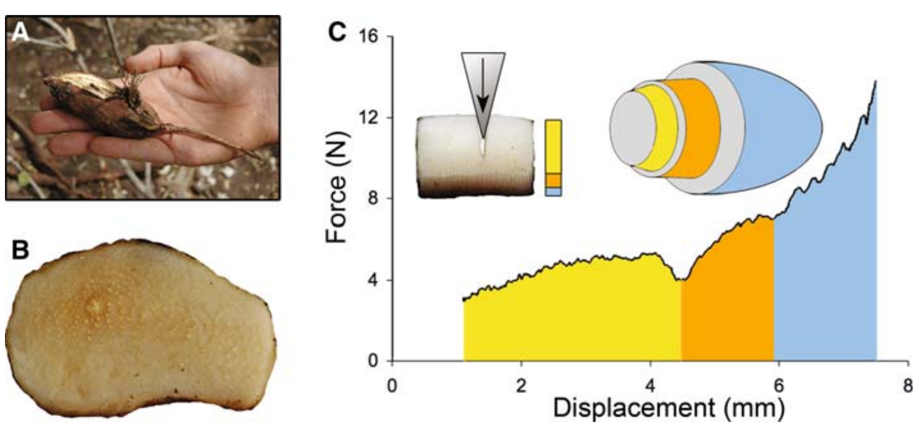

Fig. 2 Our protocol for collecting, sectioning, and wedging tubers. (**a**) The tough peridermal and cortical tissues of the shumako tuber (*Vatovaea pseudolablab*; Fabaceae). (**b**) Transverse section and parenchymatous tissue of the matukwaiko tuber (*Coccinea aurantiaca*; Cucurbitaceae). (**c**) A wedged, rectilinear specimen of the penzepenze tuber (*Vigna* sp. A; Fabaceae) with discrete parenchymatous (*yellow*), cortical (*orange*), and peridermal (*blue*) tissues. The forces (*N*) required to direct a crack through each tissue differed; hence, the work of fracture (J m^{-2}) differed

Ellery 1998; Bonyongo et al. 2000). The climate is semi-arid with ca. 500 mm of rainfall year^{-1}, occurring mostly in December–April. The corms of *Cyperus* (Cyperaceae) and tubers of *Nymphaea* (Nymphaeaceae) are a vital food for chacma baboons (*Papio ursinus*) and humans in the region (Hamilton et al. 1978; Campbell 1986). The habitat and its plant foods have also been invoked in an ecological model of hominin origins (Wrangham 2005). Plant taxonomy follows Ellery and Ellery (1997).

In August 2005 and 2006, we sampled USOs from the Western and Northern Cape Provinces of South Africa, a region of celebrated geophyte diversity (Goldblatt and Manning 2002; Procheş et al. 2005, 2006). A majority of our data was obtained from Wayland's Farm, Darling (33°S, 18°E) and private lands outside of Kamieskroon (30°S, 18°E). The vegetation of Wayland's Farm is classified as sand plain fynbos; it is exposed to rotational grazing by sheep and cattle, but it has been uncultivated for 100 years (Lovegrove and Jarvis 1986). The climate of Wayland's Farm is semi-arid with ca. 600 mm of rainfall year^{-1}, occurring mostly in April–August. Plant taxonomy follows Mason (1972) and Manning et al. (2002). Kamieskroon is in the Namaqualand winter-rainfall desert; the vegetation is classified as lowland succulent Karoo (Cowling et al. 1999). The climate is arid with ca. 150 mm of rainfall year^{-1}, although it can vary from 50 to 400 mm year^{-1}. Plant taxonomy follows Le Roux (2005).

Miscellaneous Samples

To supplement our data set, we collected the tubers of *Acanthosicyos naudinianus* and *Cucumis africanus* (Cucurbitaceae) in Hotazel (27°S, 23°E) and four specimens in the Drakensberg Mountains, Kwa-Zulu Natal Province (29°S, 29°E). *Papio ursinus* devotes 98% of dry-season foraging time to consuming corms and bulbs in the Drakensberg Mountains (Whiten et al. 1987). We also purchased a small subset of specimens from commercial trading centers, such as street markets or traditional healing shops. We omitted dried USOs from our analysis. Finally, we tested a tuber of *Dioscorea* sp. (Dioscoreaceae) from the lowland rain forest of Korup National Park, Cameroon.

Mechanical Measurements

We used a portable universal tester to estimate the Young's modulus and fracture toughness of plant tissues (Darvell et al. 1996). For all USO structures, radial samples of the edible parenchymatous tissue were cut orthogonal to the outer surface and shaped with a 4-mm cork borer into right cylinders, ca. 5 mm high. The Young's modulus, *E*, of a tissue was determined from tests on short cylinders in compression (Lucas et al. 2001; Lucas 2004). The fracture toughness, *R*, was determined with a 15°-angle wedge driven into a rectilinear-shaped

Table 2 The fracture toughness, *R* (J m^{-2}), and Young's modulus, *E* (MPa) of USOs and fruit tissues in the diets of *Pan troglodytes* and *Pongo pygmaeus*

Plant tissue	*N*-species		Mean		SE		Lower 95% CI		Upper 95% CI	
	R	*E*	*R*	*E*	*R*	*E*	*R*	*E*	*R*	*E*
USO										
Bulb	32	31	325.0^{A}	2.5^{V}	70.0	0.3	199.0	1.9	486.0	3.1
Corm	24	24	265.0^{A}	4.9^{W}	26.0	0.5	212.0	3.9	319.0	5.9
Rhizome	9	8	5448.0^{B}	11.0^{X}	2638.0	2.0	636.0	6.4	11531.0	15.7
Tuber	33	30	1304.0^{C}	5.0^{W}	228.0	0.4	841.0	4.1	1768.0	5.9
Pan fruit										
Mesocarp	12	11	81.0^{D}	1.0^{Y}	20.0	0.4	38.0	0.2	1234.0	1.8
Pongo fruit										
Mesocarp	36	36	862.0^{C}	2.7^{VZ}	130.0	0.3	598.0	2.2	1126.0	3.3
Endosperm[a]	24	13	1719.0^{BC}	4.3^{WZ}	281.0	0.5	1138.0	3.2	2299.0	5.4

N.B. orangutans occasionally consumed the bulbs of arboreal orchids, e.g., *Bulbophyllum* spp. with a fracture toughness of 270 and 726 J m^{-2} ($n = 2$ species; unpublished data)

Mean values unconnected by the same letter differ significantly

[a] The endosperm is the nutritive tissue within the protective endocarp or seed wall. The mechanical properties of a seed are therefore governed by the woody endocarp. We report the combined values of endocarp and endosperm here because the properties of both tissues are expected to exert a selective pressure on molar morphology. We use the term endosperm to convey the food tissue that orangutans appear to be selecting during foraging

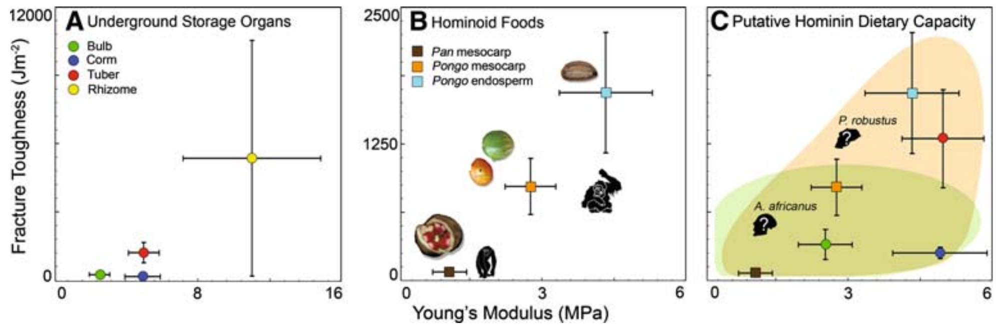

Fig. 3 Comparative mechanical data. (**a**) The parenchymatous tissue of USO forms. (**b**) The tissues of fruits in the diets of chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*); data redrawn from Vogel et al. (2008). (**c**) Overlapping data sets illustrate the mechanical similarities of some plant tissues. The hominin icons illustrate our model of USO partitioning during fallback episodes

specimen (Fig. 2). The *R* of discrete tissues was calculated by dividing the area beneath the force-deformation curve by the product of crack depth (i.e. wedge displacement) and initial specimen width (Fig. 2c). To account for anisotropic variation, we took a minimum of two measurements and averaged them.

Roasting Protocol

Hadza men used commercial matches to ignite a traditional fire (cf. Woodburn 1970, pp. 36–37). Next, they positioned each tuber in the center of the fire at the base of the flames, turning it two to three times during the roasting process. We classified a tuber as roasted when our Hadza informants perceived it as optimal for consumption. We timed each roasting event and estimated the fire temperature with a Raynger MX2 TD infrared thermometer (distance 1 m; emissivity setting 0.94; Raytek, Santa Cruz, CA, USA). We subdivided each tuber for mechanical analysis: a portion was analyzed raw (control condition) or roasted (experimental condition). This observational protocol was approved as exempt from oversight by the Institutional Review Board of the University of California Santa Cruz (no. 819).

Data Analyses

We used a Wilcoxon Signed-Rank test to determine if statistically significant variation exists among USO structures and foods in the diets of chimpanzees and orangutans (Vogel et al. 2008). Next, we used a Tukey–Kramer HSD test for multiple comparisons to determine which plant tissues differed. For all analyses, we averaged *E*- and *R*-values by plant species and in some cases plant part. All data were natural log transformed. When we compared mean values, we report the mean ± SE unless otherwise noted. All statistical procedures were performed with the statistical software JMP-SAS 6.0.3. All probability levels are two-tailed, and the significance of tests was set at alpha ≤0.05.

Results

Mechanical Properties of USOs

We sampled the USOs of 98 plant species (Appendix) and found significant variation in the Young's modulus (Wilcoxon Signed Rank test $\chi^2 = 31.95$, $df = 3$, $P < 0.0001$). Rhizomes were more resistant to deformation than all other forms, and corms and tubers were harder than bulbs (Tukey–Kramer HSD $q = 2.62$, $P < 0.05$; Table 2; Fig. 3a). A similar pattern emerged when we considered the fracture toughness of USOs (Wilcoxon Signed Rank test $\chi^2 = 42.07$, $df = 3$, $P < 0.0001$). Rhizomes were tougher than all other forms, and tubers were tougher than bulbs and corms (Tukey–Kramer HSD $q = 2.62$, $P < 0.05$; Table 2; Fig. 3a).

Table 3 The effect of Hadza roasting behavior on the fracture toughness of tubers

Species	Hadza name	Fracture toughness (J m^{-2})			
		Peridermal tissue		Parenchymatous tissue	
		Raw	Roasted	Raw	Roasted
Coccinea aurantiaca	matukwaiko			666.0	399.0
Vatovaea pseudolablab	shumako	1767.0	1322.0	300.0	138.0
Vigna frutescens	//ekwa hasa	9317.0	6288.0	4859.0	1977.0
Vigna macrorhyncha	do'aiko			659.0	356.0
Vigna sp. A	penzepenze	1855.0	1753.0	762.0	426.0

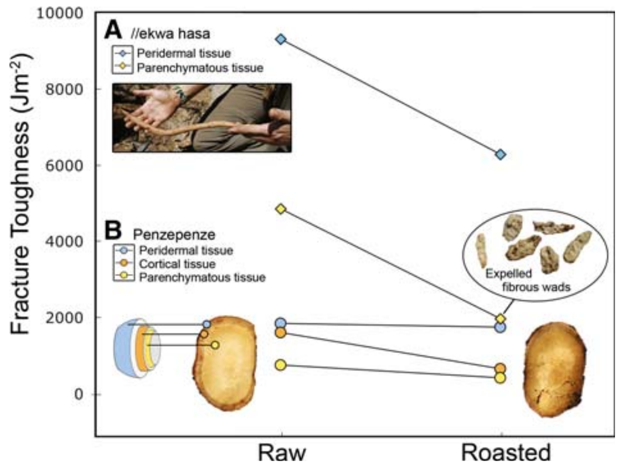

Fig. 4 The effect of roasting //ekwa hasa (*Vigna frutescens*) and penzepenze (*Vigna* sp. A) tubers. We observed that the parenchymatous tissue of //ekwa hasa was not swallowed by the Hadza after roasting; the tissue was processed orally and expelled. The cortical tissue of penzepenze exhibited disproportionately large changes in fracture toughness. Such changes permitted manual peeling of the peridermal and cortical tissues without the aid of a tool

To contextualize these results, we compared USOs to fruit tissues in the diets of chimpanzees and orangutans (Fig. 3b). Again, we found that the Young's modulus, E, and fracture toughness, R, of plant tissues differed (E: $\chi^2 = 58.60$, $df = 6$, $P < 0.0001$; R: $\chi^2 = 78.49$, $df = 6$, $P < 0.0001$). Rhizome tissues were the most resistant to deformation and fracture whereas fruit mesocarp in the diet of chimpanzees was the least resistant to deformation and fracture (Tukey–Kramer HSD, $q = 2.99$, $P < 0.05$; Table 2). Seeds consumed by Bornean orangutans tended to resemble tubers mechanically (Fig. 3c).

Effects of Roasting on Tuber Mechanical Properties

On average, the Hadza perceived a tuber as optimally edible after just 2 min of roasting (range 75–320 s). The temperature of the fire ranged from 700 to 900°C. Ethnographic accounts characterize such behavior as light roasting (Tomita 1966; Woodburn 1968); larger tubers may be roasted 5–30 min (O'Connell et al. 1999; Schoeninger et al. 2001). Overall, the edible parenchymatous tissue was less resistant to fracture after roasting (Wilcoxon Matched-Pairs Signed-Ranks Test, $P = 0.03$; Table 3). The tuber of //ekwa hasa (*Vigna frutescens*) was substantially more resistant to fracture than the other species (Table 3). We observed that the roasted parenchymatous tissue of //ekwa hasa was never fractured by the Hadza during chewing. In contrast to all other tubers, the Hadza subjected //ekwa hasa to mastication and salivary softening before they expelled a fibrous wad (Fig. 4; or quid *sensu* Schoeninger et al. 2001). Lastly, roasting had a disproportionately large effect on the toughness of the cortical tissue of penzepenze (*Vigna* sp. A; Fig. 4). This change appeared to facilitate expedient manual peeling. Unroasted penzepenze tubers were accessible only with the aid of a tool.

Discussion

> "It would seem important to distinguish types of [underground] storage organs in discussing their potential as food sources for early hominids"
> (Stahl 1984, p. 156)

Stahl was prescient. We have examined the USOs of 98 plant species and found that they differ mechanically. Rhizomes were the most resistant to deformation and fracture, followed by tubers, corms, and bulbs. This result is consistent with an earlier study of two South African species. Peters and Maguire (1981) reported that the puncture resistance of *Kirkia wilmsii* tubers was two to nine times greater than *Cyperus usitatus* bulbs. We also examined the effect of Hadza roasting behavior on five tuber species. Our results support the assumption that roasting tubers lessens the mechanical challenges of mastication, and, by inference, starch digestion. Together these findings fill an important empirical void and provide a mechanical basis for discussing the plausibility of USOs as a food source for early hominins.

With an average toughness of 5448.0 J m^{-2}, the work of fracturing rhizomes exceeds nearly all food tissues in the diets of great apes (Elgart-Berry 2004; Vogel et al. 2008). In Tuanan, Indonesia, the cambium and phloem tissues of several tree species were the toughest foods in the diet of *Pongo pygmaeus* (range 1276.0–3432.0 J m^{-2}). The orangutans devoted up to 23.0% of monthly foraging time to chewing, wadging, and expelling these tissues, and dependence was greatest during episodes of low fruit availability (Vogel et al. 2008). For *Pan troglodytes*, the pith of terrestrial herbaceous vegetation can be a similar fallback food (Wrangham et al. 1991, 1993), yet chimpanzees rarely ingest tissues as tough as those consumed by orangutans. During 58 h of observation in Kibale National Park, Uganda, we witnessed chimpanzees chewing and wadging exceptionally tough tissues only twice (*Ficus natalensis* bark = 2170.0 J m^{-2} and *Marantochloa leucantha* pith = 4223.0 J m^{-2}). Such a pattern of behavior may be instructive for assessing the plausibility of rhizomes in the diets of early hominins, particularly when combined with other lines of evidence.

For instance, stable isotope data point to the importance of C_4-derived tissues in the hominin diet. According to some estimates, such tissues represented 40% or more of the diets of *Australopithecus africanus*, *Paranthropus* *robustus*, and early *Homo* (Sponheimer and Lee-Thorp 1999; Sponheimer et al. 2005b; van der Merwe et al. 2003). Our finding that common C_4-grasses such as *Cynodon dactylon* have tough rhizomes (3770.0 J m^{-2}) raises the possibility that a diet of rhizomes contributed to the C_4 signal of some hominins and favored the evolution of large teeth and chewing muscles. The relatively immense bite force of *Paranthropus boisei* is consistent with this hypothesis (Demes and Creel 1988); however, our observations of apes and humans suggest that such tough tissues would have been chewed, wadged, and ejected from the mouth. These behaviors were unlikely to have resulted in a strong C_4 signal and we suggest that rhizomes were improbable or rare fallback foods for early hominins. The relatively untough rhizomes of aquatic plants such as *Nymphea lotus* (Nymphaeaceae) and *Phragmites australis* (Poaceae) are an exception. The rhizomes of these particular plants—and perhaps some grasses (cf. Altmann and Altmann 1970)—should be considered candidate foods for hominins (Wrangham 2005).

Tubers are more plausible hominin foods. With an average fracture toughness of 1304.0 J m^{-2} and a Young's modulus of 5.0 MPa, tubers match some of the inferred physical properties in Table 1. A broad mechanical resemblance between tubers and fruit tissues (mesocarp and seeds) in the diet of orangutans suggests that the craniodental morphology of *Pongo*—and by extension *Australopithecus* and *Paranthropus* (Walker 1981; Kay 1985; Demes and Creel 1988; Vogel et al. 2008)—is adequate biomechanically to chew tubers. In fact, some leguminous and liliaceous tubers were especially compliant. Recent reports of chimpanzees using tools and teeth to extract, wadge, and expel the parenchymatous tissue of tubers further supports their potential as a food source for early hominins (Lanjouw 2002; Hernandez-Aguilar et al. 2007). However, tuberous plants seldom use the C_4 photosynthetic pathway (Sage and Monson 1999). It is therefore unsurprising that the hair of occasional tuber-consuming chimpanzees from Ugalla, Tanzania, and bone of tuber-specialist mole rats is devoid of a C_4 signal (Schoeninger et al. 1999; Yeakel et al. 2007). Such findings do not rule out tubers from the australopithecine diet, but they do suggest that other tissues contributed to the C_4 isotopic signal of early hominins.

An important result of this study is that corms exhibit low toughness values (265.0 J m^{-2}) and relatively high Young's modulus values (4.9 MPa). This combination of mechanical properties matches many descriptions of the hominin diet as consisting of "small, hard, brittle" objects (Table 1). When compared to corms, bulbs are tougher (325.0 J m^{-2}) and more elastic (2.5 MPa). Again, this combination of traits resembles dietary inferences, especially those for *Australopithecus*. For instance, Macho et al. (2005, p. 318) suggested that the diet of *Australopithecus anamensis* was "variably hard-tough rather than hard-brittle". Similarly, the diet of *Australopithecus afarensis and Australopithecus africanus* is predicted to have been relatively tough (Scott et al. 2005; Grine et al. 2006b). In general, our mechanical data for bulbs and corms fit most authors' expectations for the physical properties of hominin foods.

Comparisons with *Pan* and *Pongo*

> "It has always been difficult to understand why man should show so many curious and detailed anatomic agreements with the orangs, in spite of the enormous differences in locomotor habits"
>
> (Gregory and Hellman 1939, p. 564)

To contextualize these results, we compared the present data set to foods in the diets of chimpanzees and orangutans. Bulbs are less elastic (harder) and substantially tougher than fruit in the diet of chimpanzees. Corms are harder still, but comparable to most seeds in the diet of orangutans (Fig. 3). These findings delimit the concept of 'hard-object feeding' and demonstrate a quantitative resemblance between the diet of *Pongo* and putative hominin foods. More than two decades ago, Walker (1981) and Kay (1985) predicted that the australopithecine diet would be similar mechanically to the diet of orangutans but substantially harder than the diet of chimpanzees. Our results support these expectations. Of course, similar patterns of dental morphology and microwear might also reflect the functional demands of sclerocarpic harvesting (sensu Kinzey and Norconk 1990) or seed-eating in particular (Jolly 1970; Peters 1987, 1993). The overall importance of seeds in the diet of early hominins is difficult to estimate. Seeds are a seasonal resource for many primate species and so a special role in driving the adaptive radiation of early hominins is unclear. Furthermore, seeds do little to resolve the C_4 conundrum that complicates our current understanding of hominin diets (Sponheimer and Lee-Thorp 2003; Peters and Vogel 2005).

Corms, Bulbs, and the C_4 Conundrum

> "The capacity to use C_4 foods may be a basal character of our lineage. We do not know, however,

which of the nutritionally disparate C_4 foods were utilized by hominids"

(Sponheimer and Lee-Thorp 2003, p. 27)

The C_4 conundrum refers to the discrepancy between dietary inferences based on stable isotopes (40% diet of C_4-grass or meat) and craniodental traits (seasonal or staple diet of small, hard, abrasive foods) (Teaford and Ungar 2000). Most functional morphologists view the blunt molar cusps and thick enamel of hominins as a poor adaptation to a diet with significant levels of grass or raw meat. Notwithstanding the challenge of acquiring meat regularly, uncooked meat is relatively tough and difficult to chew efficiently (Lucas and Peters 2000; Wrangham and Conklin-Brittain 2003). Sponheimer and Lee-Thorp (2003) called attention to this discrepancy, termed the C_4 conundrum, and attempted to resolve it by suggesting a mechanically mixed diet with C_4 input from termites, sedges, and plant USOs (Sponheimer et al. 2005a, b; Lee-Thorp and Sponheimer 2006). Our results are germane to this discussion because they frame the types of plausible USOs.

A dietary emphasis on corms and bulbs may resolve the C_4 conundrum for three reasons. First, we have shown that corms and bulbs fit the expected mechanical properties of hominin foods. They are also gritty and therefore a potential cause of the extreme wear observed on many hominin teeth—exogenous grit is uncharacteristic of most seeds. Further, the seasonal consumption of corms can result in a *Paranthropus*-like microwear pattern among chacma baboons (Daegling and Grine 1999).

Second, bulbous grasses (e.g. *Alloteropsis* spp.) and cormous sedges tend to use the C_4 photosynthetic pathway. Although C_4 photosynthesis is rare among bulb- and corm-bearing species in winter rainfall regions such as the Western Cape (Sealy 1986; Rundel et al. 1999), it is common over much of eastern and southern Africa (Sage and Monson 1999; Codron et al. 2005). In Kenya, 65% of sedges use C_4 photosynthesis (Hesla et al. 1982). In another survey, Stock et al. (2004) reported C_4 photosynthesis in 20–67% of sedges across northeast South Africa. In the same region Yeakel et al. (2007) examined the isotopic ecology of *Cryptomys*, a mole rat that consumes corms and bulbs nearly exclusively. They found that modern and Plio-Pleistocene (1.7 Ma) species exhibited δ^{13}C and δ^{18}O values that did not differ statistically from *Australopithecus africanus* or *Paranthropus robustus*. Similarly, Sillen et al. (1995) and Sponheimer et al. (2005a) called attention to the unusual combination of elevated Sr/Ca and low Ba/Ca values that *Cryptomys* shares with South African hominins. These findings demonstrate that a diet of corms and bulbs can yield a hominin-like isotopic signal.

Third, corms and bulbs are a widespread, low-fiber source of carbohydrates for which there is relatively little competition from herbivores (Conklin-Brittain et al. 2002; Laden and Wrangham 2005). For instance, iridaceous corms are an exceedingly rich source of starch ($\leq$80% dry mass; Orthen 2001) that human foragers are known to have gathered since the Late Pleistocene (Deacon 1976, 1995; Campbell 1986). In the Upper Karoo of South Africa, edible *Cyperus* and *Albuca* bulbs are prolific, with average biomasses of 7.8 and 28.0 tons ha^{-1}, respectively (Youngblood 2004). The combined weight of this evidence suggests that corms and bulbs would have been attractive foods for early hominins (Coursey 1973, Hatley and Kappelman 1980; Laden and Wrangham 2005). If we accept this contention, an outcome of this study is a revised model of resource partitioning.

Fallback Foods, USOs, and a Case for Resource Partitioning

"A hungry man does not say a coconut is too hard"

Cameroonian proverb

On the balance, the dental morphology, masticatory biomechanics, dental microwear, and stable isotope ratios of *Australopithecus* and *Paranthropus* suggest a generalized and overlapping diet (Teaford and Ungar 2000; Scott et al. 2005). As a result, there is a growing tendency to view the adaptive radiation of early hominins as the result of competition for divergent fallback foods (Ungar 2007). A differential reliance on USOs fits this model. For *Australopithecus*, the evidence indicates a fallback diet that was relatively tough and elastic—a combination of traits that characterizes bulbs (and to a lesser extent corms). For *Paranthropus*, the evidence indicates a fallback diet that was hard and brittle—a combination of traits that characterizes corms (and to a lesser extent tubers). Although tubers are also relatively tough, *Paranthropus* could probably fracture them (Demes and Creel 1988; Hylander 1988; cf. Wright 2005). Such hypothetical partitioning predicts the broad eurytopy of *Paranthropus* (Fig. 3c), but it contrasts with Robinson's (1954) influential Dietary Hypothesis, which emphasized the dietary specialization (stenotopy) of *Paranthropus*. Although both models are compatible with strong positive selection for craniodental robustness (Ackermann and Cheverud 2004), we suggest that a diet of corms and tubers most plausibly supports current evidence of scramble competition for obdurate, ubiquitous, C_4 foods amid relatively open habitats (Reed 1997; Wood and Strait 2004; Lockwood et al. 2007; Wood and Constantino 2007).

The Advantages of Roasting Tubers

> "By softening food and reducing meal size, cooking can be expected to reduce the cost of digestion… Exactly how these benefits translate into fitness has not been well established"
>
> (Wrangham 2007, p. 310)

Undomesticated tubers are generally too fracture-resistant for human consumption (mean = 1304.0 J m^{-2}). A raw carrot is relatively untough by comparison (440.0 J m^{-2}, Lucas 2004). We found that a mere 90 s of roasting resulted in large changes in tuber fracture properties. Among the five species we studied, roasting reduced the work of fracture by an average of 49% (range 40–59%). Although these data are few, they support the assumption that roasting reduces the mechanical challenge of chewing and digesting undomesticated tubers (Wrangham et al. 1999; Wrangham and Conklin-Brittain 2003). Given that Hadza women obtain 39% of their daily kcal from tubers (Marlowe 2003), a 49% reduction in chewing cost is expected to result in a significant energy gain and improved fitness. These changes alone support the adaptive advantages of cooking, but we also observed more subtle advantages.

We observed that roasting had a disproportionately large effect on the cortical tissue of penzepenze tubers (*Vigna* sp. A; Fig. 4). Roasting permitted the manual peeling of the peridermis, a tissue that is removed with a tool when the tuber is consumed raw. We suggest that an additional advantage of roasting tubers is that it speeds entry to edible tissues without the aid of tools. Such access is expected to reduce total processing costs and improve foraging efficiency, particularly for women and dependant children. Rapid roasting frees women from tuber preparation that children can perform for themselves (cf. Woodburn 1966).

Roasting also increases dietary breadth by allowing access to foods of marginal quality (Stahl 1984). For instance, with a toughness of 4859 J m^{-2} the edible tissue of //ekwa hasa (*Vigna frutescens*) surpasses nearly all foods in the diets of chimpanzees and orangutans (Vogel et al. 2008). After roasting, the toughness of the parenchymatous tissue was reduced to 1977.0 J m^{-2}. Such a value is still too excessive for fracture by human molars, and we observed that the Hadza wadged and expelled the unfractured bolus of tissue (Fig. 4). In this case, roasting softened the tuber sufficiently to permit molar occlusion, but any nutritional benefit depended on the digestive action of salivary amylase. Amylase is the sole enzyme responsible for starch hydrolysis and copy number variation of the salivary amylase gene, *AMY1*, has experienced positive selection among human populations with starchy diets, including the Hadza (Perry et al. 2007). Such evidence is lacking for chimpanzees, suggesting that an adaptive shift to chewing (and wadging) starchy foods may have favored the increased expression of salivary amylase in the human lineage.

Conclusions

The strength of any hypothesis depends on its predictive power and ability to withstand falsification from multiple lines of scientific enquiry. To date, the USO hypothesis for hominin diets has rested on ecological, morphological, and isotopic comparisons with living and fossil USO-consumers. Here we have shown that the mechanical properties of USOs agree well with hominin dietary inferences based on dental functional morphology, masticatory biomechanics, and dental microwear. We suggest a model of USO partitioning in which *Paranthropus* relied on hard-brittle C_4 corms and hard-tough C_3 tubers to a greater extent than *Australopithecus* did, which may have relied on soft-tough C_4 bulbs as a primary fallback food. Lastly, we demonstrate that roasting behavior reduces the manual and oral processing costs of consuming undomesticated tubers. These results support the adaptive advantages of roasting behavior and fill an important empirical void for evaluating the plausibility of USOs in the diets of hominins and early *Homo*.

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Appendix

Mechanical properties of plant underground storage organs

USO form, genus, and species	Family	Collection locality	Fracture toughness (J m^{-2})	Young's modulus (MPa)
Bulbs				
Albuca canadensis	Hyacinthaceae	WF	184.0	3.3
Albuca cooperi	Hyacinthaceae	WF	329.0	0.8
Albuca juncifolia	Hyacinthaceae	WF	350.0	5.0
Albuca maxima	Hyacinthaceae	K	40.0	1.4
Albuca setosa	Hyacinthaceae	WF	219.0	3.1
Albuca spiralis	Hyacinthaceae	K	87.0	1.7
Amaryllis belladonna	Amaryllidaceae	WF	600.0	0.3
Boophane disticha	Amaryllidaceae	Maun	161.0	3.2
Brunsvigia orientalis	Amaryllidaceae	WF	2293.0	2.9
Brunsvigia sp.	Amaryllidaceae	K	260.0	1.0
Crinum foetidum	Amaryllidaceae	Maun	126.0	1.1
Crinum sp.	Amaryllidaceae	HOORC	101.0	2.8
Dipcadi crispum	Hyacinthaceae	WF	451.0	0.8
Gethyllis affra	Amaryllidaceae	WF	313.0	2.4
Haemanthus coccineus	Amaryllidaceae	WF	560.0	4.7
Haemanthus crispus	Amaryllidaceae	K	247.0	2.1
Hessea chaplinii	Amaryllidaceae	WF	77.0	0.3
Lachenalia carnosa	Hyacinthaceae	K	150.0	2.7
Lachenalia mutabilis	Hyacinthaceae	WF	126.0	3.1
Lachenalia unifolia	Hyacinthaceae	WF	100.0	1.2
Ledebouria cooperi	Hyacinthaceae	D	120.0	3.2
Ornithogalum thyrsoides	Hyacinthaceae	WF	202.0	1.9
Oxalis hirta var. *tenuicaulis*	Oxalidaceae	WF	324.0	1.5
Oxalis obliquifolia	Oxalidaceae	D	183.0	–
Oxalis purpurea	Oxalidaceae	WF	437.0	1.3
Oxalis pusilla	Oxalidaceae	WF	683.0	1.7
Oxalis versicolor	Oxalidaceae	WF	606.0	2.1
Oxalis sp. A	Oxalidaceae	K	135.0	1.8
Oxalis sp. B	Oxalidaceae	K	221.0	3.6
Scilla dracomontana	Hyacinthaceae	D	336.0	3.9

Appendix continued

USO form, genus, and species	Family	Collection locality	Fracture toughness (J m^{-2})	Young's modulus (MPa)
Tulbaghia capensis	Alliaceae	WF	519.0	8.0
Veltheimia glauca	Hyacinthaceae	WF	420.0	4.1
Corms				
Babiana ambigua	Iridaceae	WF	194.0	7.2
Babiana scariosa	Iridaceae	K	362.0	7.1
Chlorophytum triflorum	Anthericaceae	WF	180.0	3.1
Cyperus alatus	Cyperaceae	MRC	288.0	8.8
Cyperus cristatus	Cyperaceae	MRC	117.0	4.7
Empodium veratrifolium	Hypoxidaceae	WF	234.0	2.3
Ferraria uncinata	Iridaceae	K	325.0	8.8
Gladiolus carinatus	Iridaceae	WF	100.0	6.2
Gladiolus gracilis	Iridaceae	WF	220.0	2.4
Hesperantha falcata	Iridaceae	WF	634.0	4.6
Ixia maculata	Iridaceae	WF	291.0	5.8
Ixia monodelphia	Iridaceae	WF	426.0	4.4
Lapeirousia jacquinii	Iridaceae	WF	86.0	3.8
Lapeirousia silenoides	Iridaceae	K	487.0	5.7
Melasphaerula ramosa	Iridaceae	WF	261.0	3.1
Moraea fugax	Iridaceae	WF	158.0	1.8
Moraea miniata	Iridaceae	K	241.0	3.6
Moraea tricolor	Iridaceae	WF	299.0	3.5
Romulea flava	Iridaceae	WF	232.0	3.4
Romulea cf. *tabularis*	Iridaceae	WF	292.0	5.7
Sparaxis bulbifera	Iridaceae	WF	269.0	12.0
Spiloxene ovata	Hypoxidaceae	WF	245.0	3.9
Wachendorffia paniculata	Haemodoraceae	WF	100.0	3.5
Watsonia coccinea	Iridaceae	WF	328.0	2.3
Rhizomes				
Bulbinella triquetra	Asphodelaceae	WF	3645.0	2.5
Cynodon dactylon	Poaceae	MRC	3770.0	14.0
Cyperus dives	Cyperaceae	HOORC	2379.0	13.7
Ficinia lateralis	Cyperaceae	WF	7967.0	13.6
Nymphea lotus	Nymphaeaceae	HOORC	414.0	–
Phragmites australis	Poaceae	HOORC	451.0	6.2

Appendix continued

USO form, genus, and species	Family	Collection locality	Fracture toughness (J m^{-2})	Young's modulus (MPa)
Schoenoplectus corymbosus	Cyperaceae	HOORC	4743.0	13.9
Willdenowia incurvata	Restionaceae	WF	25468.0	18.7
Zantedeschia aethiopica	Araceae	WF	193.0	5.5
Root tubers				
Acanthosicyos naudinianus	Cucurbitaceae	H	979.0	8.0
Arctopus echinatus	Apiaceae	WF	2758.0	2.7
Asparagus asparagoides	Liliaceae	WF	114.0	2.8
Asparagus exuvialis	Liliaceae	Maun	143.0	2.2
Asparagus rubicundus	Liliaceae	WF	296.0	1.5
Cissampelos capensis	Menispermaceae	WF	3484.0	9.2
Coccinea aurantiaca	Cucurbitaceae	Mangola	399.0	3.5
Conicosia elongata	Aizoaceae	K	874.0	4.8
Cucumis africanus	Cucurbitaceae	H	1397.0	8.3
Dioscorea sp.	Dioscoreaceae	Korup	5955.0	5.3
Eriospermum capense	Rusaceae	WF	466.0	5.4
Eriospermum nanum	Rusaceae	WF	1089.0	3.8
Eriospermum sp.	Rusaceae	K	205.0	2.6
Euphorbia tuberosa	Euphorbiaceae	WF	2080.0	3.2
Helichrysum cf. *cochleariforme*	Asteraceae	WF	916.0	2.9
Hypoxis argenta	Hypoxidaceae	D	825.0	0.8
Hypoxis hemerocallidea	Hypoxidaceae	Pretoria	1290.0	7.8
Monsonia longipes	Geroniaceae	MRC	1243.0	5.6
Nymphea lotus	Nymphaeaceae	HOORC	1139.0	5.5
Nymphea nouchali	Nymphaeaceae	HOORC	1064.0	9.4
Pelargonium seneciodes	Geraniaceae	WF	902.0	8.2
Pelargonium triste	Geraniaceae	WF	742.0	4.6
Pergularia daemia	Asclepiadaceae	Maun	2303.0	5.1
Pteronia divaricata	Asteraceae	WF	754.0	7.6
Rumex lativalvis	Polygalaceae	WF	735.0	5.9
Vatovaea pseudolablab	Fabaceae	Mangola	448.0	–
Vigna frutescens	Fabaceae	Mangola	4859.0	–
Vigna macrorhyncha	Fabaceae	Mangola	543.0	4.2
Vigna sp. A	Fabaceae	Mangola	848.0	–
Unidentified no 1	Apiaceae	MRC	1081.0	5.5

Appendix continued

USO form, genus, and species	Family	Collection locality	Fracture toughness ($J\ m^{-2}$)	Young's modulus (MPa)
Unidentified no 2	Apiaceae	MRC	679.0	4.2
Unidentified legume no 1	Leguminosae	WF	2114.0	7.0
Unidentified legume no 2	Leguminosae	WF	318.0	1.4

Collection locality key: *D* Drakensberg Mountains, *HOORC* Henry Oppenheimer Okavango Research Center, *H* Hotazel, *K* Kamieskroon (Namaqualand), *MRC* Mpala Research Centre, *WF* Wayland's Farm

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