

Sedge Foodplants Growing in the Cradle of Humankind, South Africa, and *Cyperus Esculentus* Tubers (*Patrysuintjies*)

as a C₄ Superfood

RESEARCH PAPER

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ABSTRACT

Since it was established that the early hominins of the Cradle of Humankind in South Africa ate ¹³C-enriched foods that may have included sedges with C₄ photosynthetic pathways, much work has focused on the reconstruction of hominin dietary ecologies in both southern and eastern Africa. Through the years emphasis was placed on *Cyperus papyrus* as a possible source, even inspiring an ‘aquatic diet’ hypothesis for all hominins. Baboon feeding habits and sedge regimes observed in South Africa’s ‘Lowveld’ have provided a proxy for the dietary ecology of the southern ‘Highveld’ hominins, and from the Cradle of Humankind sedges, amongst other plants, have been collected for nutritional studies. To date, however, there has been no attempt to compile an inventory of the sedge species currently growing in the demarcated area of the Cradle of Humankind. Here I list 29 Cyperaceae taxa currently recorded as growing in the Cradle of Humankind. I show that, contrary to previous inference, most of them have C₄ photosynthetic pathways and do not need aquatic ecologies or permanent wetland settings. I discuss and provide photographic records for the six species identified as current baboon and human foodplants, and highlight *Cyperus esculentus* as a possible nutritious and prolific C₄-sedge-USO food source for southern African hominins based on its energy, protein and fat/lipid profile.

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INTRODUCTION

Much has been made of stable carbon isotope studies that

provide evidence of a C₄ component in early hominin diets (e.g., Cerling et al. 2013; Ungar & Sponheimer 2011; Lee-Thorp et al. 2012; Sponheimer et al. 2013; Levin et al. 2015). Such studies often focus on the underground/ underwater storage organs (USOs) of sedges, in particular *Cyperus papyrus* (e.g., van der Merwe et al. 2008; Dominy 2012; Stewart 2014). So much so, that Wrangham et al. (2009) hypothesised that access to shallow-water aquatic habitats was not only a subsistence opportunity, but 'a necessary condition' for hominin adaptation to Savanna habitats. Yet, as Peters and Vogel (2005: 219) pointed out, most palaeo-environmental reconstructions of early hominin sites in South Africa do not support the presence of large wetlands even though carbon isotope analyses of hominin tooth enamel show 'a significant but not dominant contribution of C₄ biomass in their diets'. They suggested that the isotope signature for the Cradle of Humankind (henceforth also referred to as the Cradle) hominins could stem from a broad range of animal foraging (e.g., invertebrates, reptiles, birds, and small mammals), in combination with some C₄ plant foods; concluding that the Cradle's dryland environment probably restricted a greater reliance on a C₄ plant diet, but that elsewhere large wetlands would have offered better opportunities for such subsistence behaviour (Peters & Vogel 2005).

Although several edible C₄ grasses grow in the Cradle that may have contributed to the dietary signature (Lombard & van Aardt 2022), Peters and Vogel's (2005: 219) observations seem to agree with Sponheimer et al.'s (2005) suggestion that aquatic habitats were probably too rare in South Africa to be important sources of sedge foods, but as Caley et al. (2018: 82) point out, 'they only studied the sedges from four riverine sites located in the Kruger National Park and it remains unknown whether their conclusions are valid for the whole Limpopo catchment and larger scales'. Sedge USOs collected from the Cradle by Henry et al. (2019) showed rather high cellulose and hemicellulose values compared to various parts of other plants, and were apparently unreliable regarding antifeedant content so that the authors questioned whether the available sedge USOs may have provided an important food resource for the Cradle hominins. The full inventory of 223 foodplant taxa currently growing in the Cradle (Lombard & van Aardt 2022), however, shows that 23% of the plant parts collected and eaten by humans today are USOs – including some sedge tubers – and that 11.2% of the foodplants have C₄ photosynthetic pathways.

Herries et al. (2010) also problematised the shallowwater habitat hypothesis of Wrangham et al. (2009) for the southern hominins on meteorological and palaeoclimatic grounds. According to them, the small riverine and vleiland seasonal wetlands of the southern African interior 'are all shallow, with little open water, and dry up in winter', including those in the Cradle, and welldeveloped sedge regimes are not abundant in the riverine environments of South Africa today, so that it is doubtful that wetlands were widespread during the Plio-

Pleistocene (Sponheimer et al. 2005; Herries et al. 2010: 643). Reynolds and Kibii (2011) on the other hand, argue that the geo-morphology of the terrain around Sterkfontein Cave (Member 4), in combination with the biodiversity of its plant and animal records, suggest a riverine landscape that supported a gallery forest (also see Bamford 1999). They ascribe the presence of aquatic and wetland species in the Sterkfontein record as suggesting that 'swamps' used to exist in the region (also see Reynolds et al. 2011; Bailey et al. 2011). Another potential blow to a sedge dietary specialisation in the Cradle according to Sponheimer (2013: 231) is that 'in environments roughly analogous to the ancient Sterkfontein Valley, the vast majority of sedges use C₃ photosynthesis, so that even if the South African australopiths ate sedges, they might have needed to eat significant quantities of other C₄ foods as well'.

Trying to reconstruct sedge populations that may have been part of the hominin dietary ecology in the Cradle of Humankind is not uncomplicated. For example, Muringi and Bamford (2020) highlighted the fact that the Cyperaceae family is the most diverse in Africa. Here *Cyperus* L. represents the largest genus consisting of more than 600 species occurring in a wide range of habitats (Larridon et al., 2011). Being so numerous, and with their classifications in continuous revision (see discussion in Muringi and Bamford 2020), it may be difficult to distinguish between the species collected for palaeo-scientific research. For example, Henry et al. (2019) collected numerous sedge samples, generating some nutritional data for them, but none were identified to species level, instead they were described as *Kyllinga* sp., *Mariscus* sp., unknown big sedge (*Cyperus dives*), unknown sedge, unknown sedge 2 (very small infl), and unknown small sedge BV. In sum, as Sponheimer et al. (2013: 10315) emphasise, the ¹³C-enriched resources that hominins ate 'remain unknown and must await additional integration of existing paleodietary proxy data and new research on the distribution, abundance, nutrition, and mechanical properties of C₄ (and CAM) plants'. From the above four questions arise:

1. What is the current sedge population of the Cradle of Humankind, and what proportion of these plants has a C₄ photosynthetic pathway?
2. Do all the Cradle sedges necessarily require aquatic habitats or extensive wetlands to thrive?
3. Which of the Cradle sedge species are being used as foodplants by humans and/or primates today, and do these have C₃ or C₄ photosynthetic pathways?
4. Is there a Cradle C₄-sedge foodplant that stands out in terms of nutritional value in the way that it was claimed for *C. papyrus* in eastern Africa?

STUDY AREA AND APPROACH

To date, the dolomitic palaeo-caves located within the 51.5 thousand hectares of the UNESCO Cradle of Humankind World Heritage Site have yielded an abundant and varied hominin record, with more than 3300 fossil fragments including *Australopithecus africanus*, *A. sediba*, *A. prometheus*, *Paranthropus robustus*, and early *Homo* including *H. habilis*, *H. naledi*, *H. erectus/ergaster* and *H. sapiens* (pers. comm. Bernhard Zipfel and Stephanie Baker, 2019). Almost nowhere else do we find a similarly varied, but spatially confined fossil record spanning more than 2 Ma (Lombard & van Aardt 2022). The footprint of the Cradle of Humankind, located within the greater UNESCO Magaliesberg Biosphere, forms part of the ecotone between the Grassland and Savanna Biomes of southern Africa. The largest vegetation unit or veld type (i.e., a complex of plant communities ecologically and spatiotemporally occupying habitat complexes at the landscape scale [Mucina & Rutherford, 2011]) represented in the Cradle is the Carletonville Dolomite Grassland running through the centre of the Cradle landscape. This zone is bound by the Gauteng Shale Bushveld and Andesite Mountain Bushveld veld types to the northwest, including a narrow strip of Gold Reef Mountain Bushveld at its extreme north-western boundary. Pockets of the Moot Plains Bushveld encroach in the west, and the south-easterly boundary comprises pockets of Gold Reef Mountain Bushveld, Egoli Granite Grassland, and Andesite Mountain Bushveld (Mucina & Rutherford, 2011; [Figure 1](#)).

For plants – sedges or otherwise – to thrive in the Cradle of Humankind today they must be adapted to the summer-rainfall regime of southern Africa with heavy short-lived thunderstorms sometimes generating flash floods and raging veldfires by the end of the winter's dry season. The mean annual precipitation is lowest on the Carletonville Dolomite Grassland (593 mm) and highest in the Gold Reef Mountain Bushveld (666 mm). The annual precipitation coefficient of the area is relatively high (26–28%). The mean annual potential evaporation is much higher than the mean precipitation ranging between 2086 mm in the Andesite Mountain Bushveld and 2388 mm on the Carletonville Dolomite Grassland. As a result, the mean annual soil moisture stress levels – the percentage of days when evaporative demand is more than double the soil moisture supply – are also very high ranging from 75% to 78% of the days ([Table 1](#): all data from Mucina & Rutherford, 2011). Plant regimes are further narrowly linked to the soils or land types they grow in. I therefore provide information about these in the table below as additional context for the study area.

The vegetation units and land types ([Table 1](#)) are underlain by the ancient geology of the Cradle landscape (e.g., Carruthers

2014), and several factors suggest that the current high relief of southern Africa has been in place since ~4 Ma (e.g., Partridge et al. 2010). The plateau uplift, in combination with global patterns in climate change, brought about the shift towards the now-typical cool winters and violent summer thunderstorms (Dirks & Berger 2013). Dirks et al. (2016) showed that the low basin-averaged erosion values for the Cradle indicate an old, slow-eroding landscape that did not change much during the last 3 Ma of hominin occupation (also see Makhubela et al. 2019). The relative stability of the Cradle hominin landscape is further reflected in the development of the Grassland and Savanna Biomes of southern Africa at the transition of the Pliocene towards the Pleistocene by ~3 Ma (Carruthers 2014; Neumann & Bamford 2015). Similar to today, the Cradle landscape hosted a variety of different habitats throughout the Plio-Pleistocene, including riparian, forested, edaphic and open grassland habitats – often in combination with each other (Watson 1993; Reed 1997; Sponheimer et al. 2005; Henry et al. 2019). Between ~3 Ma and 2.5 Ma an 'El Niñolike state' may have prevailed over southern Africa, likely characterised by pulses of intense rainfall and drought (e.g., Hopley et al. 2007). After ~1.8 Ma the region became increasingly dry resulting in the proliferation of C₄-dominated grasslands (e.g., Scott 2002; Luyt & Lee-Thorp 2003; Lee-Thorp et al. 2007).

To compile a list of indigenous Cyperaceae currently growing in the Cradle that may serve as one of the proxies for palaeo-dietary reconstruction, I used Siebert and Siebert (2005), Eloff (2010), and the Flora of Southern Africa (FSA) Checklist (May 2021) provided by the South African National Biodiversity Institute (SANBI). I present basic information in terms of growth form, water dependency and distribution mainly using the

African Plant Database (<http://www.ville-ge.ch/musinfo/bd/cjb/africa/index.php?langue=an>, consulted August 2021). I also noted maximum growth-height for each plant and the altitudes at which they occur habitually. The resulting list was then systematically assessed for any species that are known foodplants from current and/or recent human foraging records and/or baboon feeding contexts, as best-fit scenarios for hypothesising about hominin diets in southern Africa (e.g., Mogg 1975; Dunbar 1976; Vincent 1985; Peters et al. 1992; Codron 2003; Codron et al. 2008; Botha et al. 2019; Welcome & van Wyk 2019; Elton & Dunn 2020; Lombard & van Aardt (2022). For each of the sedge foodplants, I provide its general distribution in southern Africa as captured on the iNaturalist Researchgrade Observations database (<https://www.gbif.org/dataset/50c9509d-22c7-4a22-a47d-8c48425ef4a7> consulted August 2021), a basic description of the plant's growth form and habitat and a brief discussion of their use as

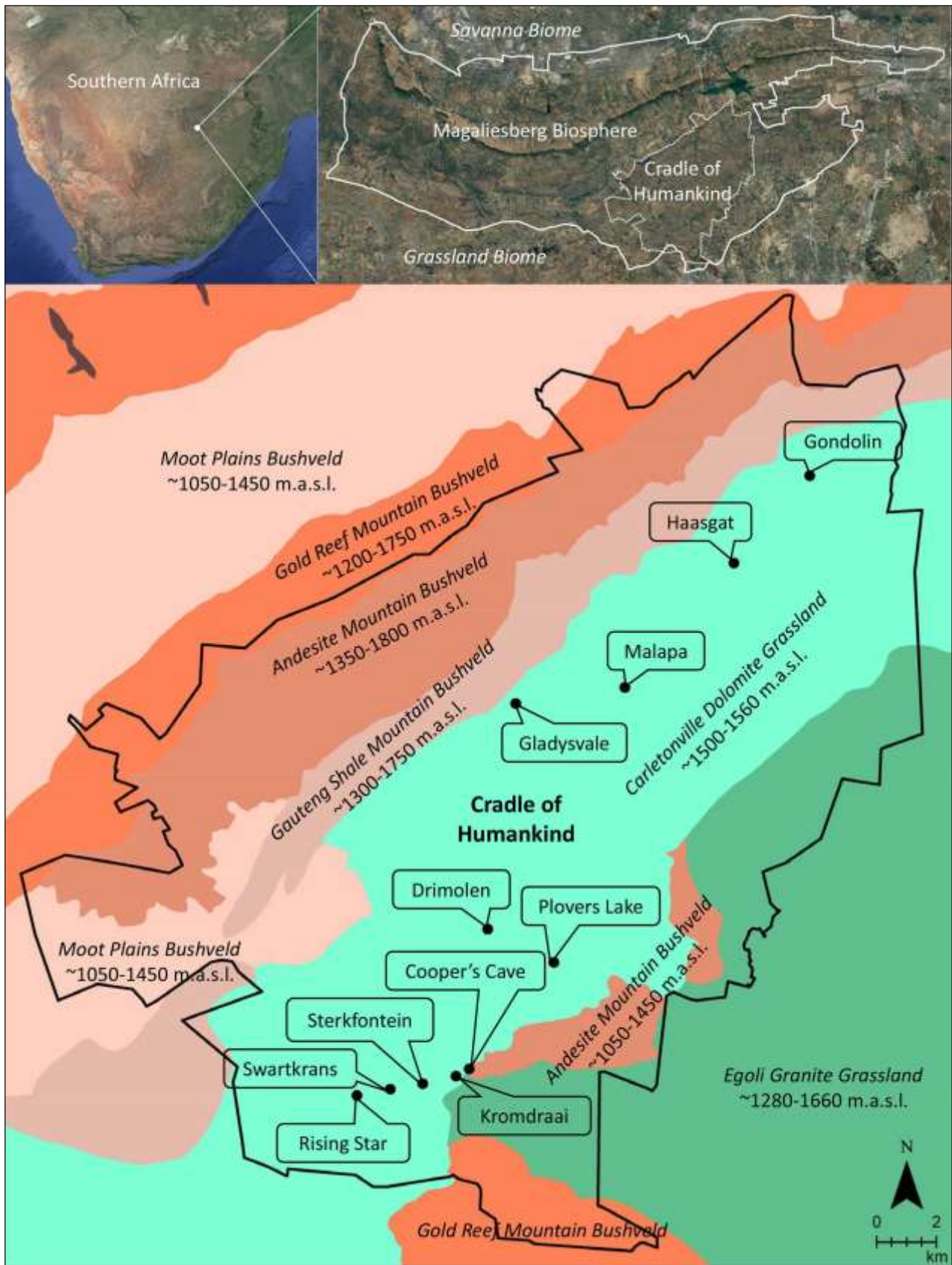


Figure 1 The footprint of the UNESCO Cradle of Humankind World Heritage Site within the Magaliesberg Biosphere and its associated veld types and approximate elevations. Background maps by Matt Caruana, University of Johannesburg.

foodplants. Finally, I highlight one of the Cradle's sedges by comparing energy, protein and fat/lipids as basic as a 'superfood' that may have contributed, amongst nutritional values amongst African USO crops as well as other things, to the C₄ signature in early hominin diet South American potatoes.

VEGETATION UNIT	MAP IN MM	APCV	MAT IN °C	# MFD	MAPE IN MM	% MASMS	LAND TYPE
Carletonville Dolomite Grassland	593	28	16.6	37	2388	78	Freely drained, red and yellow, dystrophic/mesotrophic, apedal soils comprise >40% of the land type.
Egoli Granite Grassland	682	26	16	29	2194	75	Red and yellow, dystrophic/mesotrophic, apedal soils with plintic subsoils.
Moot Plains Bushveld	636	27	17	28	2373	77	Complex profile with: a) Freely drained, red and yellow, dystrophic/mesotrophic, apedal soils; b) Black and red clays; c) Red and yellow, dystrophic/mesotrophic, apedal soils with plintic subsoils.
Gold Reef Mountain Bushveld	666	27	16.4	26	2267	76	Rock outcrops with shallow soils and lime in some of the bottomlands.
Gauteng Shale Mountain Bushveld	661	27	15.6	33	2209	76	Rock outcrops with shallow soils and lime in some of the bottomlands.
Andesite Mountain Bushveld	660	27	15.6	34	2186	76	Rock outcrops with shallow soils and lime in some of the bottomlands, and some red and yellow, dystrophic/mesotrophic, apedal soils with plintic subsoils.

Table 1 General climatic and land-type indicators for the vegetation units associated with the Cradle of Humankind (data from Mucina & Rutherford, 2011). Key: MAP = mean annual precipitation, APCV = annual precipitation coefficient of variation, MAT = mean annual temperature, MFD = mean frost days with a screen temperature below 0°C, MAPE – mean annual potential evaporation, MASMS = mean annual soil moisture stress.

CYPERACEAE GROWING IN THE CRADLE OF HUMANKIND

There are currently 29 taxa belonging to 12 genera in the Cyperaceae family on record as growing in the Cradle of Humankind, one of which is not indigenous to southern Africa, namely *Carex acutiformis*. Ehrh. (Table 2). Perennial plants dominate the population with only two (*Bulbostylis humilis* and *Isolepis cernua*) being annual. The *Cyperus* genus is best represented (n = 11, 39%), followed by *Carex* (n = 4, 14%), *Bulbostylis* (n = 3, 11%), *Scleria* and *Kyllinga* are both represented by two (7%) species in the Cradle, whilst the *Fimbristylis*, *Fuirena*, *Isolepis*, *Pycurus*, *Schoenoplectus* and *Schoenoxiphium* genera each only have one species currently recorded for the Cradle (Figure 2a). Some of these lineages have considerable time depth, for example *Bulbostylis* dates back to 14.9 ± 4.7 Ma, *Cyperus* to 9.7 ± 1.3 Ma, and *Fimbristylis* to 9.1 ± 3.2 Ma (Besnard et al., 2009; Larridon et al., 2013; Sage, 2017), so that most of the Cyperaceae growing in the Cradle today could have been part of the Plio-Pleistocene hominin dietary ecology.

All the plants, bar two from the *Carex* genus (i.e., *C. rhodesiaca* and the non-indigenous *C. acutiformis*), are listed as having cyperoid growth forms – thus, being true sedges (Table 2). Amongst them, three (10%) are also classified as geophytes (i.e., *Cyperus esculentus*, *Cyperus rotundus* and

Scleria bulbifera), that is plants with growth forms that include specifically modified stem or root systems for the storage of energy or water in the form of tubers, corms, rhizomes, or bulbs (see Beentjie 2016) (Figure 2b). Cumulatively, at least 15 (52%) of the Cradle Cyperaceae have C₄ photosynthetic pathways as opposed to the 12 (41%) with C₃ pathways. For two *Cyperus* species I could not find information about their pathways (i.e., *C. austro-africanus* and *C. uitenhagensis*), but, even if they both turn out to have C₃ pathways, C₄ sedges are still best represented on the Cradle landscape today (Figure 2c).

When it comes to the relationship of the Cradle sedges with water, only two (7%) are emergent hydrophytes that habitually grow in shallow water (i.e., *Cyperus sexangularis* and *Schoenoplectus brachyceras*), and *Fuirena stricta* is the solitary aquatic, sudd hydrophyte that grows rooted in an impenetrable mass of floating vegetable matter. Helophytes – plants typical of marshy or lake-edge environments (sometimes also salty), in which the USOs are generally submerged in soil or mud with the aerial shoots protruding above the surface – comprise 41% of the Cradle's Cyperaceae, with *Fimbristylis dichotoma* also able to thrive in drier settings. However, more than half (55%) of the Cradle's Cyperaceae taxa are mesophytes. These plants are adapted to neither particularly dry nor particularly wet environments needing only moderate amounts of water. Different from hydrophytes and helophytes, they typically avoid soils with standing and/ or salty water (Table 2; Figure 2d).

Unlike *Cyperus papyrus*, an emergent sudd hydrophyte that grows up to 4.5 m tall and at altitudes of 7–1000 m.a.s.l., most

of the Cradle's sedges never grow more than a metre tall, with only three taxa (i.e., *Cyperus fastigiatus*, *C. leptocladus* and *C. sexangularis*) ever reaching 1.5 m or more. Tiny species never growing taller than ~30 cm include *Bulbostylis humilis*, *Cyperus*

rupestris, *C. uitenhagensis* and *Isolepis cernua* (Figure 2e). Most of the sedges growing in the Cradle never outgrow the surrounding grasses, and several of them are grass-like,

SPECIES/TAXA	GROWTH FORM & PATHWAY	WATER DEP.	MAX HGHT	ALTITUDE	DISTRIBUTION
<i>Abildgaardia ovata</i> (Burm.f.) Kral	Perennial herb, cyperoid, C ₄	Mesophyte	490	180–1830	BOT, ESW, NAM, EC, FS, GA , KN, LP, MP, NW
<i>Bulbostylis burchellii</i> (Ficalho & Hiern) C.B.Clarke	Perennial herb, cyperoid, C ₄	Mesophyte	490	180–1830	BOT, ESW, NAM, EC, FS, GA , KN, LP, MP, NW
<i>Bulbostylis humilis</i> (Kunth) C.B.Clarke	Annual herb, cyperoid, C ₄	Mesophyte	250	10–2955	BOT, ESW, NAM, EC, FS, GA , KN, LP, MP, NC, NW , WC
<i>Bulbostylis oritrephes</i> (Ridl.) C.B.Clarke	Perennial herb, cyperoid C ₄	Mesophyte	450	200–2200	LES, ESW, EC, FS, GA , KN, LP, MP, NW
<i>Carex acutiformis</i> Ehrh.	Perennial herb, emergent hydrophyte, C ₃	Helophyte	800	0–2440	Not indigenous , but occurs in LES, EC, FS, GA , KN, MP, NW , WC
<i>Carex cognata</i> Kunth	Perennial herb, cyperoid, C ₃	Helophyte	800	10–2000	BOT, ESW, LES, NAM, EC, FS, GA , KN, LP, MP, NW , WC
<i>Carex rhodesiaca</i> Nelmes	Perennial herb, emergent hydrophyte, C ₃	Helophyte	600	610–2225	ESW, LES, EC, GA , KN, LP, MP
<i>Carex uhligii</i> K.Schum. ex C.B.Clarke	Perennial herb, cyperoid, C ₃	Mesophyte	600	120–1510	EC, FS, GA , KN, LP, MP, NW , WC
<i>Cyperus austro-africanus</i> C.Archer & Goetgh.	Perennial herb, cyperoid	Mesophyte	910	45–1731	ESW, NAM, EC, GA , KN, LP, MP, NW
<i>Cyperus congestus</i> Vahl	Perennial herb, cyperoid, C ₄	Helophyte	910	2–2425	BOT, ESW, LES, NAM, EC, FS, GA , KN, LP, MP, NC, NW , WC
<i>Cyperus esculentus</i> L. var. <i>esculentus</i>	Perennial herb, geophyte, cyperoid, C ₄	Mesophyte	100	5–2100	BOT, ESW, LES, NAM, EC, FS, GA , KN, LP, MP, NC, NW , WC
<i>Cyperus fastigiatus</i> Rottb.	Perennial herb, cyperoid, C ₄	Helophyte	2590	5–1735	EC, FS, GA , KN, LP, MP, NC, NW , WC
<i>Cyperus leptocladus</i> Kunth	Perennial herb, cyperoid C ₃	Mesophyte	1750	393–2035	ESW, GA , KN, LP, MP, NW
<i>Cyperus margaritaceus</i> Vahl var. <i>margaritaceus</i>	Perennial herb, cyperoid, C ₄	Mesophyte	750	12–2100	BOT, ESW, NAM, FS, GA , KN, LP, MP, NC, NW
<i>Cyperus obtusiflorus</i> Vahl var. <i>obtusiflorus</i>	Perennial herb, cyperoid, C ₄	Mesophyte	450	5–1770	BOT, ESW, LES, EC, GA , KN, LP, MP, NW
<i>Cyperus rotundus</i> L.	Perennial herb, geophyte, cyperoid, C ₄	Mesophyte	650	5–1370	BOT, ESW, NAM, EC, GA , KN, LP, MP, NC, NW , WC
<i>Cyperus rupestris</i> Kunth var. <i>rupestris</i>	Perennial herb, cyperoid, C ₄	Mesophyte	150	200–2375	ESW, LES, EC, FS, GA , KN, LP, MP, NC, NW
<i>Cyperus sexangularis</i> Nees	Perennial herb, cyperoid, emergent hydrophyte, C ₃	Helophyte	1500	15–1500	BOT, ESW, EC, GA , KN, LP, MP, NC, NW
<i>Cyperus uitenhagensis</i> (Steud.) C.Archer & Goetgh.	Perennial herb, cyperoid	Mesophyte	300	20–2000	ESW, LES, EC, FS, GA , KN, LP, MP, NW , WC
<i>Fimbristylis dichotoma</i> (L.) Vahl subsp. <i>dichotoma</i>	Perennial herb, cyperoid, C ₄	Mesophyte / Helophyte	1260	10–1675	BOT, ESW, NAM, EC, FS, GA , KN, LP, MP, NW
<i>Fuirena stricta</i> Steud. var. <i>stricta</i>	Perennial herb, cyperoid, sudd hydrophyte, C ₃	Helophyte	750	105–1670	BOT, ESW, NAM, GA , KN, LP, MP, NW , SWZ
<i>Isolepis cernua</i> (Vahl) Roem. & Schult. var. <i>cernua</i>	Annual herb, cyperoid, C ₃	Helophyte	200	3–1830	LES, NAM, EC, FS, GA , KN, LP, MP, NC, NW , WC
<i>Kyllinga alba</i> Nees	Perennial herb, cyperoid, C ₄	Mesophyte	520	85–2000	BOT, ESW, LES, NAM, EC, FS, GA , KN, LP, MP, NC, NW
<i>Kyllinga melanosperma</i> Nees	Perennial herb, cyperoid, C ₄	Helophyte	1000	5–1675	BOT, ESW, EC, GA , KN, LP, MP, NW

<i>Pycreus unioloides</i> (R.Br.) Urb.	Perennial herb, cyperoid, C ₄	Helophyte	700	25–1950	BOT, ESW, LES, EC, GA , KN, LP, MP, NW
<i>Schoenoplectus brachyceras</i> (Hochst. ex A.Rich.) Lye	Perennial herb, cyperoid, emergent hydrophyte, C ³	Helophyte	500	850–2000	ESW, EC, FS, GA , KN, LP, MP, NW
<i>Schoenoxiphium sparteum</i> (Wahlenb.) C.B.Clarke	Perennial herb, cyperoid, C ₃	Mesophyte	600	30–2000	ESW, LES, EC, FS, KN
<i>Scleria bulbifera</i> Hochst. ex A.Rich.	Perennial herb, cyperoid, geophyte, C ₃	Mesophyte	600	150–2070	ESW, EC, GA , KN, LP, MP, NW
<i>Scleria dregeana</i> Kunth	Perennial herb, cyperoid, C ₃	Helophyte	800	610–1950	BOT, ESW, LES, EC, GA , KN, LP, MP

Table 2 Cyperaceae currently growing in the Cradle of Humankind. Key: BOT = Botswana; ESW = Eswatini; LES = Lesotho; NAM = Namibia; EC = Eastern Cape, South Africa; FS = Free State, South Africa; GA = Gauteng, South Africa; KN = KwaZulu-Natal, South Africa; LP = Limpopo Province, South Africa; MP = Mpumalanga, South Africa; NC = Northern Cape, South Africa; NW = Northwest Province, South Africa; WC = Western Cape, South Africa.

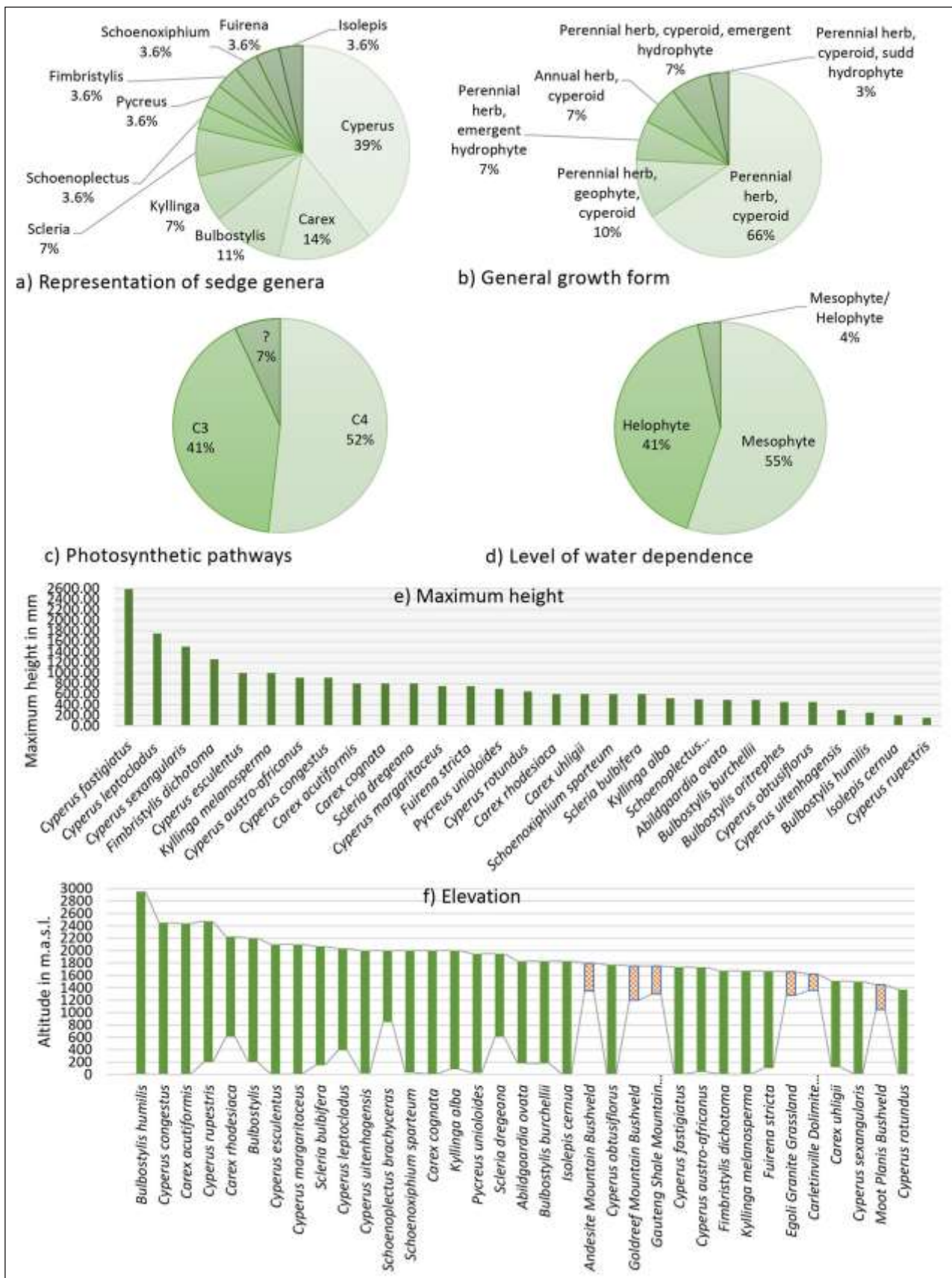


Figure 2 Aspects of the current Cyperaceae population of the Cradle of Humankind. **a)** Percentages of C₃ vs C₄ photosynthetic pathways represented. **b)** Percentages of genera represented amongst the Cradle's sedges. **c)** Aspects of the growth forms represented. **d)** Levels of water dependence represented wherein helophytes require aquatic conditions and mesophytes usually avoid growing in the water-logged soils and can thrive in dryland ecologies. **e)** The maximum heights to which the different

Cyperaceae of the Cradle grow. **f**) The general elevations at which the different Cyperaceae of the Cradle grow with the textured bars indicating the elevation of the vegetation units.

so that they easily disappear within their surroundings. The veld types associated with the Cradle of Humankind (Figures 1 and 2f; see Mucina and Rutherford, 2011), range in altitude from ~1050 to ~1750 m.a.s.l., and all the sedges currently growing there have altitude ranges that fit these vegetation units with *Carex uhligii*, *Cyperus rotundus* and *C. sexangularis* perhaps limited to the lowerlaying areas of the Cradle landscape (Figure 2f). Based on these data, we could probably rule out both *Cyperus papyrus* and the 'unknown big sedge', identified by Henry et al. (2019) as possibly being *Cyperus dives*, as growing in the Cradle of Humankind. Both these species usually grow at altitudes of ≤ 1000 m and neither has yet been identified as indigenous to the high-altitude grasslands of the Gauteng and Northwest Provinces of South Africa where the Cradle is located. Also, if the plateau uplift happened at ~4 Ma, it may be that these species were not around since the Plio-Pleistocene transitional period associated with the appearance of the hominins.

FOODPLANT SEDGES OF THE CRADLE OF HUMANKIND

From the list above (Table 2), three species have been recorded in the context of baboon feeding, two of which are also foraged and eaten by humans, and three more by humans only. At least six of the Cradle's current Cyperaceae species can therefore be identified as potential hominin food sources. *Bulbostylis burchellii* (Ficalho & Hiern) C.B.

Clarke (Figure 3) is a small, grass-like perennial sedge with a C_4 pathway that is prolific in Gauteng, South Africa, where it grows amongst the grasses on rocky ridges (e.g., Bredenkamp & Theron 1978; Bredenkamp et al. 2006). It is adapted to an environment with little water, making it a hardy, drought-resistant, densely tufted plant, growing from a delicate woody rhizome. Marais (2005) recorded baboons feeding on its roots during the winter in the Blyde River Canyon (Mpumalanga, South Africa). Little else seems to be known about this species in terms of its suitability as a foodplant. Its observation as a baboon food source during the dry winter, however, together with its hardiness and proliferation in the Cradle region may warrant further exploration as a fallback food when other more luscious sources have been depleted.

Cyperus congestus Vahl (Figure 4. Previously: *Mariscus congestus*, commonly known as dense flat-sedge or clustered flat-sedge, and in South Africa as hedgehog sedge) is a perennial, facultative palustrine wetland plant, that grows as a grass-like sedge with a C_4 pathway (e.g., Sonnenberg & Botha 1992; Verloove 2014). As an emergent narrow-leaved aquatic plant, its habitats include damp stream banks, moist depressions in grasslands, and the margins of temporary waterbodies throughout much of South Africa (van Ginkel & Cilliers 2020; also see Gordon-Gray et al. 2006). The sweetish, crisp USOs have a slightly astringent juice, and light roasting improves their flavour. They are an important food source of the !Kung hunter-gatherers of Namibia (e.g., Story 1958; Marshall 1976; Fox & Norwood Young

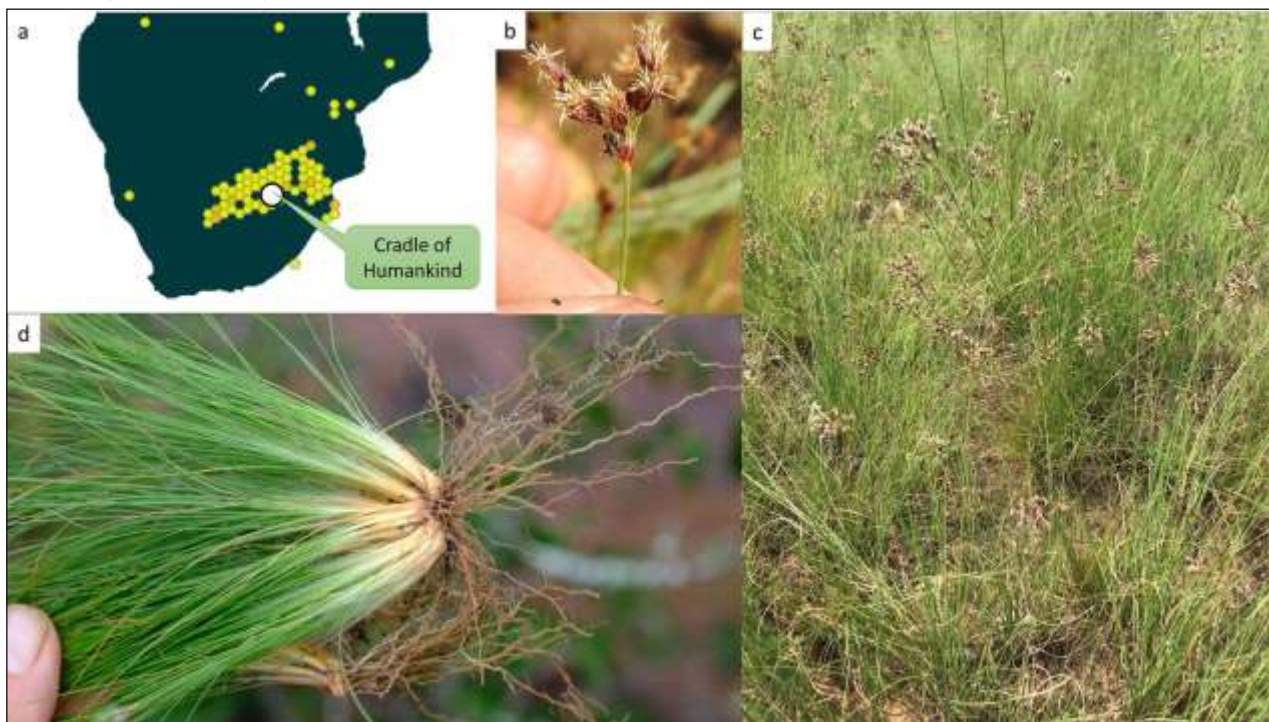


Figure 3 *Bulbostylis burchellii* (Ficalho & Hiern) C.B. Clarke. **a**) Distribution in southern Africa (<https://www.gbif.org/species/5292413>); **b**) inflorescence (photo by Matthew Fainman); **c**) growing in the veld (photo by David Hoare); **d**) rootstock (photo by Nick Helme). All photographs are licensed for use under <http://creativecommons.org/licenses/by-sa/4.0/>.

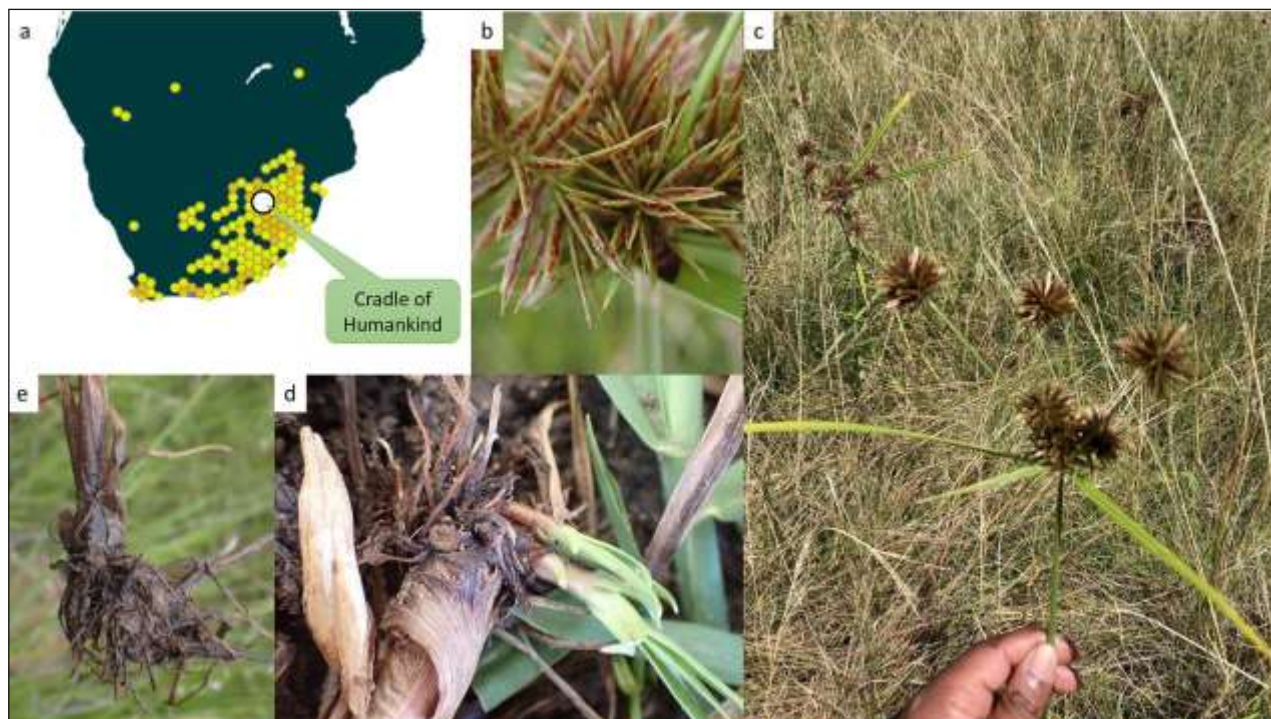


Figure 4 *Cyperus congestus* Vahl. **a**) Distribution in southern Africa (<https://www.gbif.org/species/2714656>); **b**) inflorescence (photo by David Hoare); **c**) growing in the veld (photo by Namhla); **d** & **e**) rootstock and USO (photos by David Hoare). All photographs are licensed for use under <http://creativecommons.org/licenses/by-sa/4.0/>.

1982), and in the Eastern Cape, South Africa, Bhat et al. (2002) recorded how the leaves are pulled from the ground and the white part of the plant consumed as a wild vegetable found year-round near riverbanks.

Cyperus esculentus L. (Figure 5). A.k.a. yellow nutsedge, earth almond, chufa, tiger nut; in South Africa *patrysuinjie*) may have been part of the *Paranthropus boisei* diet in eastern Africa (e.g., Macho 2014). It is a perennial cyperoid herb with a C_4 pathway, needing only a moderate amount of water. The USOs are sweet with a nutty flavour and is used as a vegetable in southern Africa and elsewhere (Watt & Breyer-Brandwijk 1962). For example, herd boys, women and children of the high-altitude uKhahlamba-Drakensberg and Lesotho grasslands eat the raw or baked tubers that are available year-round (Vinnicombe 1976; Fox & Norwood Young 1982, and see Mabogo 1990 for an account from the Limpopo Province). Nama-speaking people of Namaqualand and Namibia also eat the lower stem raw or roasted (Archer 1994), whilst in both Namibia and South Africa, the tubers are sometimes pounded and stirred with water into a paste, to which milk and honey is added. Mixed with a grain porridge, it provides a delicious and hearty meal (von Koenen 2001; Roberts & Roberts 2017). Further north in Africa the wild USOs are foraged, cleaned and sold in markets as ‘tiger nuts’, and in west Africa the plant is cultivated for its sweet corms in the context of milk production and making fortifying gruels (Roberts & Roberts 2017). As one of the earliest cultivated crops in ancient Egypt, it was used widely, perhaps because as little as 150–200 g of USO tissue

satisfies the human daily requirements for lipid/fat intake (Eteshola & Oraedu 1996; Dominy 2012).

Cyperus rotundus L. (Figure 6. A.k.a. purple nutsedge) is a perennial, grass-like sedge with a C_4 pathway, preferring dry conditions but will tolerate moist soils. Similar to *C. esculentus* its tubers somewhat resemble ‘nuts’. The plant is widespread throughout Africa, growing in almost every soil type, humidity, and pH, but not in the shade or soils with a high salt content, and perhaps not in the higher lying mountainous regions. Its robustness earned it the reputation as ‘one of the world’s worst weeds’ (e.g., Holm et al. 1977). The tubers are edible raw or cooked (e.g., Tanaka 1976; Lim 2016). It is one of the sedges most often recorded in the context of baboon USO feeding in eastern Africa (e.g., Swedell et al. 2008; Schreier 2010; Bentley-Condit & Power 2018). Soaking the tuber will overcome its hardness, and the bitterness is reduced by drying it for a few days before consumption (Lim 2016). The dried tubers can be ground into a powder and used as a cereal (Moerman 1998), and the tiny seeds of this sedge are also edible (Kunkel 1984). The USOs have been recorded in southern Africa as food foraged by both the Topnaar of Namibia and the Kalahari !Kung hunter-gatherers (Van damme et al. 1922; Lee 1979). In western Africa the slightly fragrant tubers are gathered and chewed by herdsmen and boys (Irvine 1952). There are several archaeological reports for *C. rotundus* as a foodplant. For example, tuber remains from Wadi Kubbania, Egypt, at ~18 ka, and microfossils from human dental calculus from AI

Khiday, Central Sudan, at ~7 ka (e.g., Buckley et al. 2014; Dwyer 2016).

plants of southern Africa associated with palustrine and riverine wetlands where it grows along the edges of pans, rivers

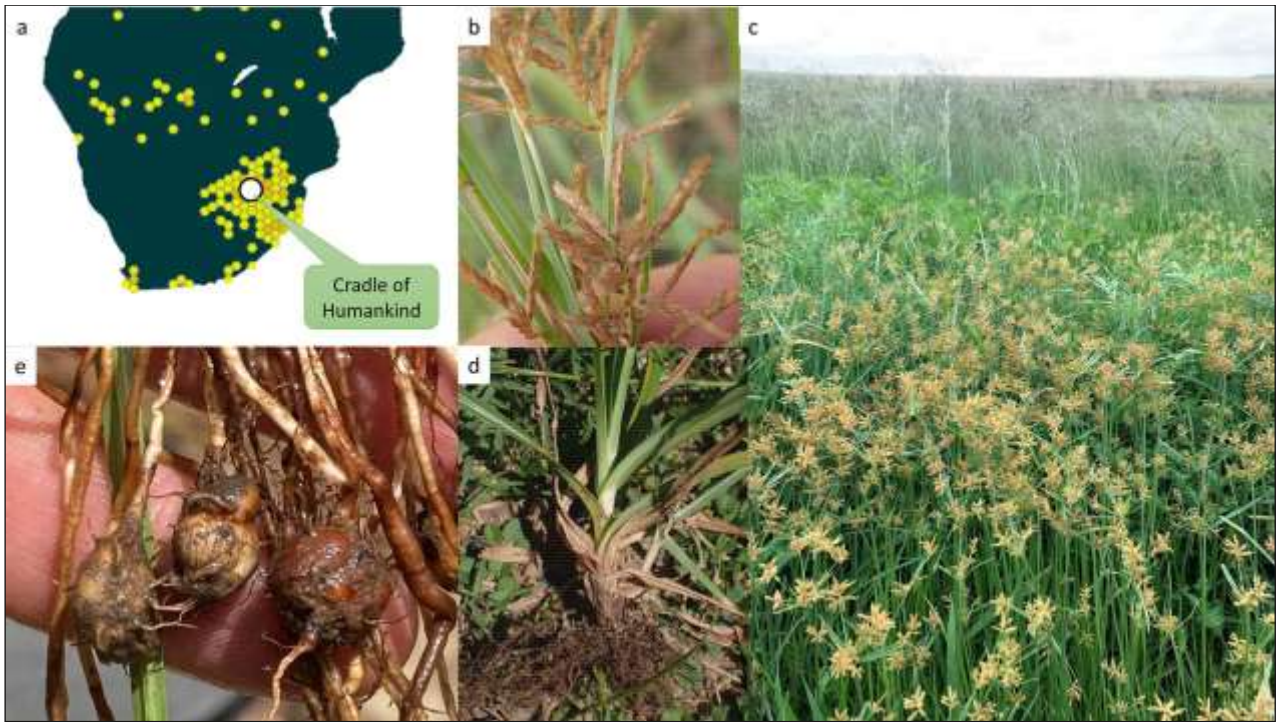


Figure 5 *Cyperus esculentus* L.: **a)** Distribution in southern Africa (<https://www.gbif.org/species/2716226>); **b)** inflorescence (photo by David Hoare); **c)** growing in the veld (photo by Dave Richardson); **d)** culm and stalk (photo by David Hoare); **e)** rootstock and tubers (photo by Dan Spaulding). All photographs are licensed for use under <http://creativecommons.org/licenses/by-sa/4.0/>.



Figure 6 *Cyperus rotundus* L.: **a)** Distribution in southern Africa (<https://www.gbif.org/species/2714818>); **b)** inflorescence (photo by Yael Orgad); **c)** growing in the veld (photo by David Hoare); **d)** inflorescence closeup; **e)** rootstock (photos by Bry Celee). All photographs are licensed for use under <http://creativecommons.org/licenses/by-sa/4.0/>.

Cyperus sexangularis Nees (**Figure 7**) is the only taxon amongst the Cradle sedge foodplants that has a C_3 photosynthetic pathway and is also the tallest – growing up to 1500 mm. It is a robust, tufted grass-like cyperoid herb belonging to the emergent narrow-leaved aquatic

and streams, often rooted in wet/watery substrates, but occasionally also found in drier soils (van Ginkel & Cilliers 2020). San hunter-gatherer children would uproot and eat the young shoots, while still enfolded in their basal sheaths, drawing out the soft pith between their teeth (Smith 1966).

Kyllinga alba Nees (Figure 8) is a small robust, densely tufted, grass-like cyperoid herb with a C₄ pathway needing only a moderate amount of water. The USO is eaten by children in Kenya (Ichikawa 1987; Mutie et al. 2020), and baboons from the Laikipia Plateau, Kenya, also eat the flower/seed heads (Barton et al. 1993). In southern Africa, the roots are traditionally used as



Figure 7 *Cyperus sexangularis* Nees: **a**) Distribution in southern Africa (<https://www.gbif.org/species/2716106>); **b**) inflorescence (photo by Kate Braun); **c**) growing in the veld (photo by Vuyiswa Sithatu); **d**) young shoots (photo by David Hoare); **e**) stem cross section (photo by Wynand Uys); **f**) inflorescence closeup (photo by David Hoare). All photographs are licensed for use under <http://creativecommons.org/licenses/by-sa/4.0/>.

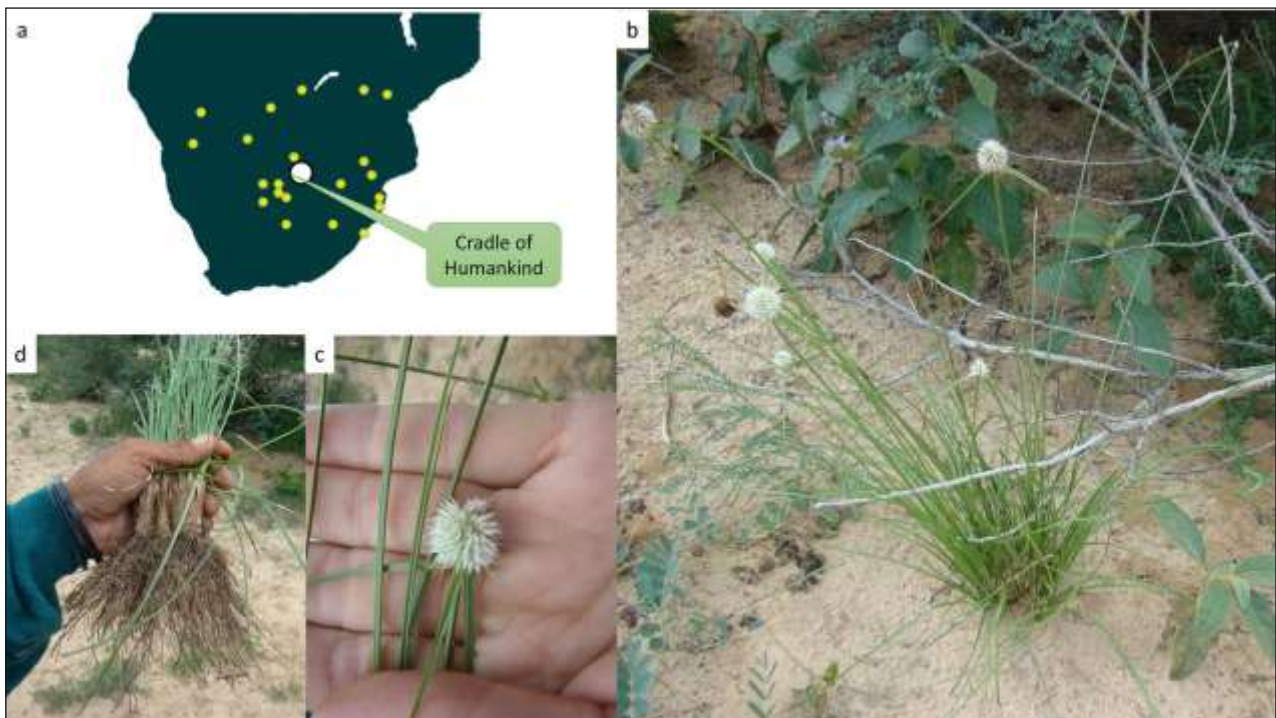


Figure 8 *Kyllinga alba* Nees: **a**) Distribution in southern Africa (<https://www.gbif.org/species/2718781>); **b**) growing in the veld; **d**) inflorescence; **e**) rootstock. All photographs by Christfried Naumann from http://en.wikipedia.org/wiki/Public_domain.

stoppers in ostrich eggshell bottles, possibly because of antibacterial properties that keep the water fresh, and the pleasant fresh taste the roots give to the water (van Wyk & Gericke 2000).

CYPERUS ESCULENTUS (PATRYSUINTJIES) IN TERMS OF ENERGY, PROTEIN AND FAT

Of the six foodplants above, the USOs of *Cyperus esculentus*, elsewhere also known as ‘tiger nuts’, stand out as a contemporary ‘superfood’ (e.g., Vega-Morales et al. 2019). The plant may well have been available during the Plio-Pleistocene in sub-Saharan Africa considering that its bio-geographical history indicates a dispersal from Africa with the most recent common ancestor between *C. esculentus* taxa dating to 5.1 Ma (de Castro et al. 2015). In South Africa and Namibia one of the Afrikaans names for this plant is *patrysuintjie*. *Uintjie* (pronounced /'e'ki/ or /'œ'ki/) is a general term used by the local populations (including the Khoe-San) for a number of Cyperaceae and Iridaceae species known for their edible USOs. Thunberg (1794–5) recorded the vernacular as deriving from the Dutch word for onion (*ajuin*), used in the 1600s by Van der Stel for corms (in this instance *Moraea edulis* [now *M. aristata*]) eaten by the indigenous Khoe people living at the Cape of Good Hope when the Europeans first arrived there (Smith 1966). Most of the *uintjie* species subsequently received descriptive names based on a special characteristic. In the case of *C. esculentus*, *patrys* = partridge, refers to the fact that guineafowl and other indigenous partridge species enthusiastically scratch for the tubers whenever they can find them (e.g., Roberts & Roberts 2017). The keen ethological eye of hunter-gatherer women and children would undoubtedly find patches of *C. esculentus* on their foraging forays by observing bird behaviour – much in the same way they find honey (e.g., Guy 1972; Kahn & Weiss 2017). For the southern African context, *patrysuintjie* is therefore a more accurate and appropriate vernacular than ‘tiger nut’, seeing that there were/are no wild tigers in sub-Saharan Africa, the USOs have nothing to do with nuts botanically, and it acknowledges their status as indigenous, pre-colonial Khoe-San food source.

Today, *C. esculentus* is an important crop of the Spanish Mediterranean where the tubers are used to produce a refreshing milk-like beverage called *horchata de chufa* (Mosquera et al., 1996). Spain and other European countries also import tons of cultivated *C. esculentus* tubers from African countries such as Nigeria, Niger, Mali, Senegal, Ghana, the Ivory Coast and Togo. In these countries they are mostly used as an uncooked vegetable or side dish (e.g., Omode et al. 1995), but in Nigeria similar to Spain, it is used to make *kunnu*, a non-alcoholic beverage sometimes also prepared from cereals such as millet and sorghum. Here, Belewu and Abodunrin (2008) showed that whilst the energy content of *kunnu* prepared from *C. esculentus* tubers, millet and sorghum were similar, the

sedge-corm drink had the highest percentages of fat and protein, and that it was the most palatable.

The plant is also cultivated in American countries such as Chile, Brazil and the USA in Louisiana, Missouri, New Mexico and Florida where it is mainly used to supplement animal feed (Sánchez-Zapata et al. 2012). Although *C. esculentus* is still considered a weed in many countries (e.g., De Vries 1991; Adejuyitan 2011; Ukwuru et al. 2011; Lauwers et al. 2020), it is now widely recognised as a ‘health food’. For example, the tubers are considered to help prevent heart disease, diabetes and thrombosis, activate blood circulation, and assist in the treatment of gastrointestinal diseases and/or reducing the risk of colon cancer (Borges et al. 2008; Adejuyitan et al. 2009; Chukwuma et al. 2010; Sánchez-Zapata et al. 2012; Kiyashko et al. 2020). Below, I explore the nutritional values of *C. esculentus* tubers sourced from various markets in Africa mostly provided by subsistence farming in terms of energy, protein, and fat/lipids to assess their potential as C₄-USO food source within the dietary ecology of the Cradle of Humankind (also see Supplementary file 1).

As hominin brain sizes increased, they also progressively required foods with a high energy, protein and fat/lipid yield (e.g., Aiello & Wheeler 1995; Milton 1999; Ben-Dor et al. 2011). The current daily requirement for energy in adult humans is ~8400 kJ, for protein 46–56 g, and for fat 44–77 g (e.g., National Health Services, UK). In terms of energy (kJ/100 g), all the *C. esculentus* samples are in the top 50% of a sample of 71 different USO foods (Figure 9a). They group favourably with peanuts (*Arachis hypogaea*) as the top energy-USO crop (e.g., Eshun et al. 2013; Mustapha et al. 2015), Yams (*Dioscorea* spp.) (e.g., Lewu et al. 2010; Adepoju et al. 2018; Ezeabara & Anona 2018; Erena & Alemu 2019), *Vigna frutescens* a tuber eaten by Hadza foragers in Tanzania (e.g., Schoeninger et al. 2001), African potatoes (*Hypoxis* spp.) (e.g., Wadley 1978; Otonola & Afolayan 2019), and *C. rotundus* or purple nutsedge (e.g., Wehmeyer 1986; Ibrahim et al. 2013; Etilib et al. 2016; Ikon et al. 2020). The five African *C. papyrus* samples, on the other hand, are all in the bottom 50% together with potatoes (*Solanum tuberosum*) (e.g., Wehmeyer 1986; Jimenez et al. 2015), *Cladium mariscus* (e.g., Sievers 2015), and the Cradle-sedge USOs tested by Henry et al. (2019).

Protein values for both *C. esculentus* and *C. Papyrus* are variable, with that of the 15 *C. esculentus* samples ranging between 3.3 and 9.7 g/100 g (mean = 5.2, SD = 1.9, median = 5), which is generally higher compared to that of five available *C. papyrus* samples ranging from 0.5–7 g/100 g (mean = 3.7, SD = 2.9, median = 4.1) (Figure 9b). *C. esculentus* USOs (together with peanuts) stand out, however, in terms of fat/lipid content amongst

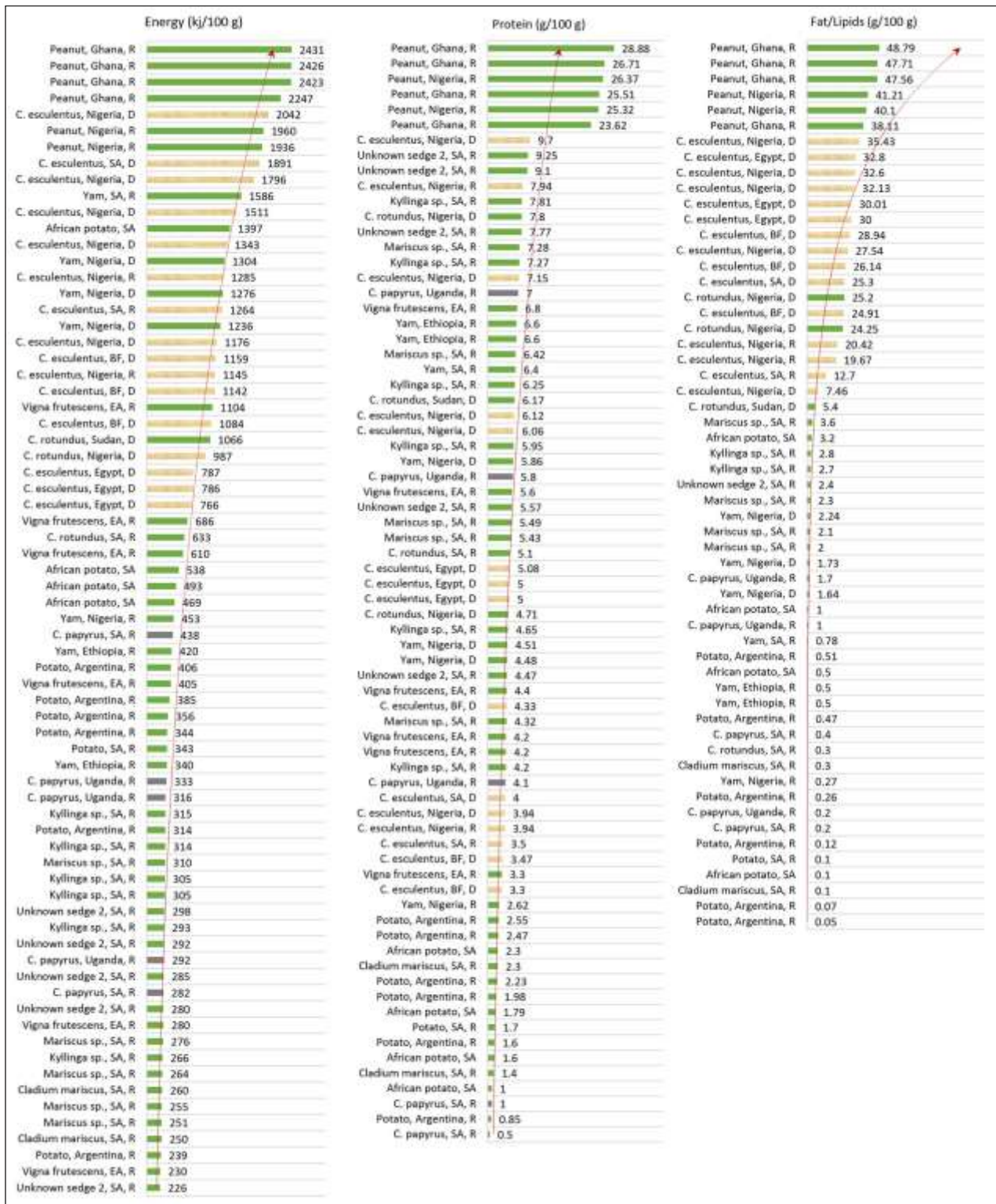


Figure 9 Energy, protein and fat/lipid values of *Cyperus esculentus* (golden bars) compared to *Cyperus papyrus* (grey bars) and other USO foods from Africa and potatoes from Argentina (green bars). For the energy values I use kilojoules, converting values that were originally published in Kilocalories or carbohydrates into the approximate kilojoules using the relevant Google calculator. Key to abbreviations: R = raw, D = dried. See Supplementary file 1 for raw data.

all the other samples, with *C. rotundus* the only another Cradle sedge with two samples amongst the top 40% out of the 54 samples in total (Figure 9c). By contrast, all the *C. papyrus* samples fall within the bottom 40% in terms of their fat/lipid nutritional values. Collectively, these data demonstrate that *C. esculentus* or *patrysuintjies* are consistently more nutritious – and in terms of both energy and fat/lipid content exponentially so – compared to *C.*

papyrus and domesticated potatoes that up to now served as standard for ‘high nutrient quality’ amongst the potential hominin sedge-USO foods (e.g., Wrangham et al. 2009 following Van der Merwe et al. 2008).

In terms of bioavailability (the fraction of an ingested nutrient that reaches systemic circulation), Codina-Torella et al. (2015) showed that *C. esculentus* tubers have low tannin and phytate levels. Tannins are known to interfere with the

bioavailability of some nutrients in the intestinal track, decreasing their absorption, and low levels may indicate good digestibility, especially for proteins (e.g., Glew et al. 2006; Okoye & Ene 2018). Phytates can form insoluble complexes with minerals such as calcium, iron, potassium, magnesium, zinc and manganese, causing reduction in bioavailability and absorption of such minerals in the body. Its relative low levels in *C. esculentus* tubers limit such reduction so that these minerals can be absorbed (Codina-Torella et al. 2015). *C. esculentus* oil contains high proportions of oleic acid, which is considered high-quality oil in terms of digestibility or bioavailability (Guo et al. 2021). Guo et al. (2021) also found that the content of unsaturated fatty acids is considerably higher than saturated fatty acids so that *C. esculentus* oil is an edible oil with an excellent fatty acid composition.

C. esculentus tubers produce 47.9% of its weight as digestible carbohydrates (Addy & Eteshola 1984), and a low-digestible viscous starch (Li et al. 2017). According to Li et al. (2017) such starches are gaining interest because they are related to the improved metabolism of lipids and cholesterol, and pre-biotic effects on the microbiome of the colon where they ferment and become more digestible. They also show benefits regarding low glycaemic response, causing satiety and improved physical performance and glucose tolerance, as well as reduced blood lipid level and insulin resistance (Li et al. 2017; also see Grabitske & Slavin 2008). The total digestible nutrients in four *C. esculentus* tuber varieties from Turkey ranged from 71.59% to 73.78% (Ayaşan et al. 2020). Bioavailability levels will vary contextually, but the existing information generally shows good systemic availability for the nutrients contained in *C. esculentus* tubers. Relatively little is known about the bioaccessibility (the amount of an ingested nutrient that is available for absorption in the gut after digestion) of *C. esculentus* tubers, and further *in vivo* studies

are needed to evaluate this aspect (e.g., Moral-Anter et al. 2021).

In terms of biomass, the tuber dispersal of *C. esculentus* is profuse. In a single year's growth, one 'mother tuber' can produce more than 1900 shoots and up to ~6900 tubers in an area of 3.2 m² (Tumbleson et al. 1961; Jordan-Molero & Stoller 1978; Lauwers et al. 2020). Depending on circumstance, the tubers may lie dormant for several years at a depth of up to 20 cm (Stoller et al. 1973; Lauwers et al. 2020), so that even during times of extreme drought or after destructive veldfires, when the aerial parts of the plants are dry or ruined, the corms are protected and remain a reliable food source. The fact that the nutritious USOs grow from thin roots, some distance from the culm (Figure 10a), may be one of the reasons why this sedge foodplant has not yet been collected or reported on from the Cradle of Humankind or other areas in southern Africa as possible hominin dietary source. When collectors are unfamiliar with the ethno-historical use of foodplants in the region and their growth habits, it is easy to miss *patrysuintjies* because they often break off from the brittle roots when pulled from the soil or when the collecting strategy is too shallow – resulting in a culm with roots but no tubers (Figure 10b). Sometimes the USOs are only pea-sized, making them even more difficult to find and collect for study (Figure 10c).

CONCLUDING DISCUSSION

At the beginning of this contribution, I identified four questions arising from previous literature that may benefit from an inventory of the sedge species currently growing in the Cradle of Humankind, and from an understanding of the human use of indigenous foodplants in the region. The first question pertains to the sedge population and its proportion of plants with C₄



Figure 10 *Cyperus esculentus* USOs: a) Corms growing from thin, brittle roots several centimetres below the culm (photo by Dan Spaulding). b) Culm and rootstock collected without corms (photo by David Hoare). c) Pea-sized corms that can be easily missed during collection (photo by J.M. Neiva). All photographs are licensed for use under <http://creativecommons.org/licenses/by-sa/4.0/>.

photosynthetic pathways. Here I demonstrated that the Cradle currently has a recorded sedge population of 29 species, which is considerably more, and more diverse, than the six sedge groups recently collected and studied by Henry et al. (2019). At least half of them have C_4 photosynthetic pathways. These results from the high-altitude Grassland-Savanna ecotone of the Cradle landscape itself contrasts notably with the 28% of C_4 sedges reported by Sponheimer et al. (2005) for the comparative low-altitude Savanna Biome of the Kruger National Park, South Africa. Using the inventory provided here, future studies can now focus on the actual sedge population growing in the Cradle of Humankind for the reconstruction of the local hominin dietary ecology, instead of relying on proxies from locations with completely different vegetation units – such as the Kruger National Park (see Mucina & Rutherford, 2011 for differences in vegetation units between the Cradle of Humankind and the Kruger National Park) – or small-scale plot sampling within the Cradle that cannot accurately or fully assess the vegetation richness of the landscape. Importantly, the notion that the Sterkfontein Valley may have contained a preponderance of C_3 sedges (much more so than their C_4 counterparts) can be rejected as a working hypothesis for the dietary ecology of the Cradle's hominins.

The second question asked whether all the sedges growing in the Cradle necessarily require aquatic habitats or extensive wetlands to thrive. In this context, I established that more than half of the Cradle's Cyperaceae taxa are mesophytes that thrive without needing permanent, extensive wetland ecologies. Instead, most species are mesophytes, and therefore well adapted to the Cradle's ecology with its seasonal fluctuation in precipitation and for thriving in drier substrates. The current Cradle sedge data therefore reveal that a shallow-water ecology is not a requirement for all African sedge regimes – consequently drawing into question the inference that access to shallow-water aquatic habitats was 'a necessary condition' for all hominin adaptation to the Savanna and/or Grassland Biomes of sub-Saharan Africa as suggested by Wrangham et al. (2009).

Thirdly, I asked which of the sedges growing in the Cradle are known human and/or primate foodplants, and whether these have C_3 or C_4 pathways. I identified six of the Cradle's Cyperaceae species as known baboon and/or human foodplants used throughout sub-Saharan Africa. Five of them have C_4 pathways. This outcome contradicts Sponheimer's (2013) suggestion that, especially in terms of the foodplants available to hominins in the Sterkfontein Valley, the 'vast majority' was C_3 sedges. What is more, only two of the USO-sedge foodplants are 'wetland' plants, the rest being well-adapted to the drier, summerrain conditions of the Cradle landscape. Thus, by focussing on the sedges actually growing in the Cradle, and through insight provided by the ethno-historical records of the use of foodplants in southern Africa, it becomes clear that local non-aquatic sedges may have directly contributed to the C_4 signatures observed in the diets of the

South African hominins – even if other components added to such a signature (e.g., Peters & Vogel 2005).

Lastly, I wanted to explore whether there is a Cradle C_4 -sedge foodplant that stands out in terms of nutritional value in the way that it was claimed for *C. papyrus* in eastern Africa by van der Merwe et al. (2008) and Wrangham et al. (2009). By comparing the nutritional values in terms of energy, protein and fat/ lipids, I could highlight the local *patrysuintjies* or the USOs of *Cyperus esculentus* as a C_4 -sedge foodplant that exceeds the nutrition potentially provided by *C. papyrus* to early hominins. In fact, only a few hands full of these sweet-tasting raw corms easily fulfils the current daily requirement for energy, protein and fat/lipids in adult humans – something that *C. papyrus* cannot do.

Unlike *C. papyrus*, *patrysuintjies* do not grow in wetland or aquatic ecologies, instead they thrive amongst the grasses on drier ground, well-adapted to withstand the cyclic drought and fire regimes of the high-altitude Cradle ecotone landscape.

Whilst *C. esculentus* is a likely candidate for a staple food in the Cradle, it is equally important not to ignore the greater nutritional landscape (e.g., Henry et al. 2019). The full inventory (n = 223) of the Cradle's foodplant taxa (Lombard & van Aardt 2022), highlights the most species-rich foodplant families such as the Poaceae, Apocynaceae, and Fabaceae. It shows that the Cradle's geophytic foodplants are dominated by the Apocynaceae, which is in contrast with the Cape Fynbos region where the high geophyte frequency is largely ascribed to the Iridaceae (Welcome & Van Wyk, 2019). The Cradle's foodplant population also contains a good proportion of non-geophytic plants (i.e., plants without specifically modified root systems such as tubers, corms, rhizomes, or bulbs) with growth forms that range from perennial trees to annual herbs whose USOs or roots are known to be eaten (for species and discussion see Lombard & van Aardt 2022). Most of these plants require further investigation in terms of their potential nutritional potential – as well as their (including *C. esculentus* tubers) mechanical properties to assess how they align with Cradle-hominin tooth microwear (e.g., Scott et al. 2005; Grine et al. 2012; Ungar et al. 2008; Casteren et al. 2020).

However, with their evolutionary time depth of more than 5 Ma, and their extraordinary ability to generate a prolific and nutritious geophytic biomass year-round, *C. esculentus* tubers may well have provided a dependable superfood to the Cradle's hominins, as they still do to many Africans today, as well as to the world's rapidly growing health-food industry. I therefore suggest that future studies may benefit from exploring the phytolith characterisation of *C. esculentus*, the potentially tool-assisted foraging strategies that would have enabled hominins to access the corms, as well as testing the outcomes presented here with further dental microwear and isotopic research. My own exploration will continue into fine-grained macro- and micro-nutrient analyses of *C. esculentus* and the potential adaptive benefits access to such plants and their nutrients may have provided the hominins who roamed the Cradle of Humankind landscape.

ADDITIONAL FILE

The additional file for this article can be found as follows:

- **Supplementary File 1:** Data for USO nutrition. DOI: <https://doi.org/10.5334/oq.110.s1>


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COMPETING INTERESTS

The author has no competing interests to declare.

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