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ORIGINAL ARTICLE

Variability and preservation biases in the archaeobotanical record of *Eleusine coracana* (finger millet): evidence from Iron Age Kenya

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Abstract
Eleusine coracana (finger millet) is a nutritious and easily storable grain that can be grown in unfavourable environments and is important to the food security of millions of farmers in Africa and South Asia. Despite its importance and promise as a sustainable crop for smallholders in the Global South, its history remains poorly understood. *Eleusine coracana* has only rarely been recovered from archaeological sites in the region of Africa where it was domesticated and never in quantities large enough to study its evolution under cultivation. Here we report on a large assemblage of Iron Age (ca. 900–700 cal BP) *E. coracana* grains recovered from Kakapel rock shelter in western Kenya. We also carried out carbonization experiments on modern grains in order to directly compare these archaeological specimens to extant landraces. We found that finger millet is only well preserved when carbonized at temperatures lower than 220 °C, which may contribute to its scarcity in the archaeological record. *Eleusine coracana* shrinks but does not significantly change shape when carbonized. When corrected for the effects of carbonization, the *E. coracana* grown by Iron Age farmers at Kakapel was smaller grained than modern landraces, but is nonetheless identifiable as domesticated on the basis of grain shape and surface texture. A comparison with other Iron Age *E. coracana* reveals considerable variation in the grain size of landraces cultivated during this era. This is the largest quantitative morphometric analysis of *E. coracana* grains ever conducted, and provides a basis for the interpretation of other archaeological populations. This assemblage is also the first evidence for *E. coracana* cultivation in western Kenya, a biodiversity hotspot for landraces of this crop today.

Keywords Finger millet · Eleusine coracana · Eastern Africa · Archaeobotany · Carbonization · Preservation bias · Morphometrics · Iron Age

Introduction

Domestication of cereals in Africa can be traced to two general regions, the Sahara/Sahel and the highlands of eastern Africa. In the western Sahara/Sahel, *Pennisetum glaucum* (pearl millet) was domesticated by ca. 4,500 BP in the Tillemsi valley (Manning et al. 2011) and *Oryza glaberrima* (African rice) by 2,300 BP in the inland Niger delta (Murray 2004). In the eastern Sahel, *Sorghum bicolor* (sorghum) with intermediate morphology between wild and domesticated dating to ca. 6,000 BP has recently been reported from Sudan (Winchell et al. 2017; Barron et al. 2020). *Eragrostis tef* (tef) was domesticated in highland Ethiopia by early Aksumite times, ca. 2,000 BP (D'Andrea 2008). Of the major African cereal crops, only the domestication of *Eleusine coracana* (finger millet, ragi, korakan) remains mysterious, with very little archaeobotanical evidence from its likely region of origin. *E. coracana* is a highly nutritious and easily storable grain crop that can be grown in marginal environments and is important to the food security of millions of farmers in Africa and South Asia (Belton and Taylor 2004; Gupta et al. 2017). Despite its importance and promise as a sustainable crop for smallholders in the Global South, its history

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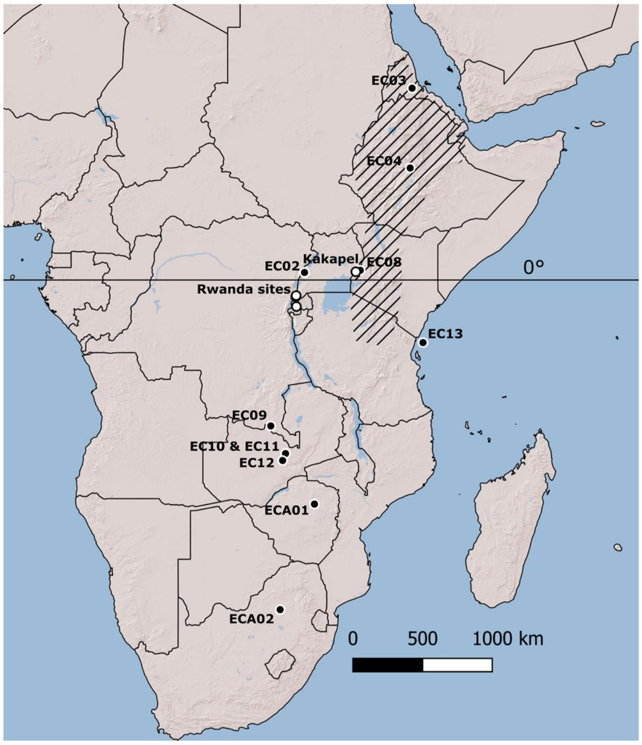

Fig. 1 Map of study area. Shaded area indicates the likely region of domestication for finger millet (Harlan 1971; Hilu and de Wet 1976a, b; Hilu et al. 1979). Archaeobotanical assemblages analysed in this study are indicated by white dots and collection sites for modern landraces and wild accessions are marked by black dots and labelled with codes listed in Table 2

remains poorly understood. Based on the distribution of the wild progenitor and landrace diversity, it was probably domesticated somewhere in the highlands stretching from Ethiopia through Uganda and western Kenya into northern Tanzania (Fig. 1; Hilu and de Wet 1976a, b; Harlan 1971). But *E. coracana* has only rarely been recovered from archaeological sites in this region, and then never in quantities large enough to study its evolution under human management. Here we report on a large Iron Age assemblage of 52 well-preserved *E. coracana* grains[1] from three contexts dating between 900 and 700 cal BP from Kakapel rock shelter in highland western Kenya (Fig. 1). This assemblage is significant for two reasons. First, it provides a rare glimpse of the morphology of an ancient landrace within the region where finger millet was domesticated. Second, it provides the first archaeological evidence for its cultivation in western Kenya, which is today one of its centres of diversity (Dida et al. 2008; Manyasa et al. 2015).

We also report the results of carbonization experiments with *E. coracana*. These allow us to provide correction factors for comparing ancient carbonized assemblages with a newly compiled comparative sample of grains from modern eastern African landraces, and also to suggest that preservation bias may be working against the recovery of archaeological *E. coracana*. Seeds change shape and size when carbonized, and the magnitude and direction of these changes depends on the chemical composition of the seed and its moisture content as well as the temperature and duration of exposure to heat (Wright 2003; Mueller 2017). Some taxa have narrow ranges of conditions that will result in carbonized specimens that are well enough preserved to be identified; others can be preserved under a wide range of conditions (Boardman and Jones 1990; Märkle and Rösch 2008). Until these hidden biases are understood, taxa that are poorly preserved by carbonization may be misinterpreted as unimportant to ancient agricultural systems and diets (Wright 2008).

Eleusine coracana in the archaeological record

Eleusine coracana was probably domesticated in the highland regions between the Lake Victoria basin and

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[1] Technically, these are caryopses: the dry, one-seeded *fruits* of a grass. We will use the more commonly understood words "grain" or "seed" interchangeably with caryopsis in this paper for the sake of clarity. Likewise, the diagnostic surface textures of these grains, described below and illustrated in Fig. 2, are those of the adhering caryopsis coat. We will use "grain surface texture" or caryopsis coat to describe this feature (Esau 1965, p. 592).

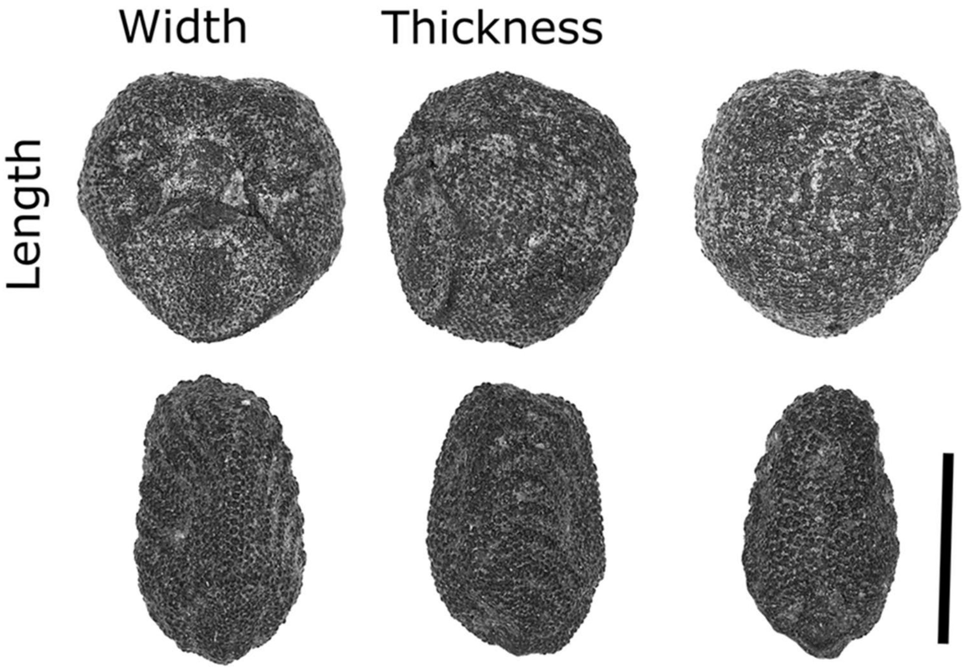

Fig. 2 Ventral, lateral and dorsal views of well preserved grains from Iron Age contexts at Kakapel, showing dimensions measured for this study. Measurements of shape and area were taken from ventral view, far left. Top row, *E. coracana*; bottom row, the wild progenitor *E. coracana* ssp. *africana*; scale bar = 1 mm

the Horn of Africa (Fig. 1; Hilu and de Wet 1976b), but archaeobotanical evidence for *E. coracana* in Africa is extremely limited and all solidly dated assemblages are within the past 2,000 years. There must be earlier evidence to be found, since the earliest *E. coracana* in India dates to ca. 4,000 BP (Fuller 2006; Boivin and Fuller 2009; Boivin et al. 2014). Genetic evidence has shown that Indian landraces are more closely related to those from lowland regions of Africa to the east of the highlands where it was probably domesticated (Fig. 1), suggesting a further time delay between its domestication and arrival in India to accommodate the differentiation of lowland landraces (Dida et al. 2008). Most previously reported archaeobotanical *E. coracana* from highland eastern Africa comes from Ethiopia. Phillipson reported a large assemblage of *E. coracana* from Gobedra cave, which he interpreted as dating to the 3rd millennium BCE on the basis of associated pottery (Phillipson 1977). Microphotographs of this perfectly preserved desiccated *E. coracana* were included in a widely cited early overview of its archaeobotany, along with the uncertain early date (Hilu et al. 1979). A direct radiocarbon date on this sample obtained several years later indicated an age for this assemblage of only 1,179–492 cal BP (OxA-741, 820 ± 200 BP) (Gowlett et al. 1987; Reimer et al. 2020), but because the erroneous earlier dates are much more accessible, they are still frequently cited in plant breeding literature (Dida et al. 2007; Gimode et al. 2016). At Ona Nagast, a single damaged grain was dated by association to the early Aksumite period (ca. 2,000 cal BP), and three more were recovered from post-Aksumite contexts (ca. 1,300–1,100 cal BP) (D’Andrea 2008). At Aksum itself, two *E. coracana* grains were recovered from an extraordinarily rich late Aksumite domestic context dating to 1,400–1,200 cal BP (Boardman 2000; Phillipson 2000). Outside Ethiopia, but also within the likely region of origin, a single grain of wild *E. coracana* ssp. *africana* was recovered from Gogo Falls, on the eastern shore of Lake Victoria, associated with pre-Iron Age Kansyore pottery (Lange 1991). The archaeological layers at Gogo Falls are interpreted as being fairly mixed, making the exact age of this find unclear (Robertshaw 1991). A single grain of domesticated *E. coracana* was recovered from a pit associated with a pastoral Iron Age occupation dated to 1,300–1,000 cal BP at the Deloraine site, in the central Rift Valley of southern Kenya (Ambrose et al. 1984). Recent archaeogenetic research has identified this site to be the first place where West African ancestry associated with Bantu people is evident in this region of eastern Africa (Prendergast et al. 2019).

Just outside the highland region where *E. coracana* was probably domesticated, in south-eastern Sudan, *Eleusine* sp. grain and chaff impressions were identified on potsherds from Kashim el Girba, Mahal Teglinos and Jebel Mokram. These may be remains of wild *E. coracana* (cultivated or gathered), and are dated by associated pottery to between ca. 5,500 and 2,000 BP (Beldados 2016). Further afield, one grain was tentatively identified as cf. *E. coracana* at Kursakata, on Lake Chad in northeastern Nigeria, from a level dated to ca. 2,000 cal BP (Klee et al. 2000). To the south and east, Walshaw (2010) recovered a single grain each from the coastal Tanzanian sites of Tumbe and Chwaka, ca. 1,300–500 cal BP. Crowther et al. (2016, 2018) report *E. coracana* from middle to late Iron Age contexts at four sites on the coast of southern Kenya and Indian Ocean island sites, Panga ya Saidi (n = 1) and Mgombani (n = 30), Tumbe on Pemba, (n = 1), and Sima on Comoros (n = 1). *E. coracana* has been recovered from three Iron Age sites in Rwanda, Karama (n = 4), Musanze (n = 19), and Nguri cave (n = 8), dating between 1,400 and 800 cal BP. A total of 20 measurable grains were identified from assemblages at these sites, with a maximum of seven from any single site (Giblin and Fuller 2011). Before this study, the Rwanda assemblages were the largest and only archaeobotanical assemblages of *E. coracana* from Africa for which measurements are available.

The Kakapel assemblage reported here thus nearly triples the total number of analysed ancient *E. coracana* grains that have been reported and is the largest archaeobotanical assemblage of this crop ever recovered from a site in eastern Africa. It is important to note, in addition to this thin archaeobotanical record, that *E. coracana* has conspicuously *not been recovered* from sites where it might be expected to occur, even when researchers did thorough archaeobotanical sampling. For example, at the major Iron Age earthwork of Munsa, Uganda, 230 flotation samples did not yield any *E. coracana* (Young and Thompson 1999). Likewise, none was recovered in pre- or early Aksumite contexts at Aksum, despite extensive sampling (Boardman 2000). Research by the Sealinks Project in coastal eastern Africa recovered *E. coracana* from only four sites, despite flotation of > 7,430 L of sediment from a total of 16 sites, which produced only 33 *E. coracana* specimens from > 2,440 crop remains (Crowther et al. 2016). The scarcity of *E. coracana* remains in the archaeobotanical record suggests that preservation biases may be at work, a possibility that we explored experimentally for this study.

Genetic insights into *E. coracana* domestication and diversification

While we have very little archaeobotanical information about where and when *E. coracana* was domesticated and how it subsequently diversified and spread within Africa, significant insights have come from genetics and particularly from the efforts of plant breeders to characterize diversity in its landraces in the last two decades. *E. coracana* is an annual tetraploid species in the genus *Eleusine*, which includes nine other annual and perennial species, eight of which are native to Africa, nomenclature according to Tropicos (2020). The direct progenitor of finger millet is *Eleusine coracana* ssp. *africana*, which is also a tetraploid annual grass native to Africa. This species resulted from a hybridization between *E. indica*, a widely naturalized, weedy diploid annual and another diploid species of *Eleusine,* possibly either *E. floccifolia* (Hilu and Johnson 1992; Bisht and Mukai 2001) or *E. tristachya* (Zhang et al. 2019). While *E. coracana* and its wild progenitor are closely related and can readily hybridize, they diverged into two distinct clades when *Eleusine* was domesticated. *E. coracana* ssp. *africana* has significantly more genetic variation, suggesting that the size of the founding population of domesticated *Eleusine* was small compared to that of its wild progenitor (Dida et al. 2007, 2008; Gimode et al. 2016). Wild and domesticated *E. coracana* are also easily differentiated by phenotype, including the grain characteristics illustrated in Fig. 2, among many other characters of the whole plant that are not usually preserved in the archaeological record (Dida et al. 2008).

Because they are constantly evolving, domesticated plants and animals cannot be maintained in a consistent form without an equally consistent management regime or formal breeding. Variation within domesticated taxa should be of interest to archaeologists because it reflects the ways human communities transmit knowledge and skills through institutions and relationships in which novices become experts through learning and socialization (Lavé and Wenger 1991; Nazarea 2005), as well as reflecting gene flow by the exchange of seeds between communities (Pautasso et al. 2013). The genetic and phenotypic diversity of landraces has long been appreciated by plant breeders and conservationists because it makes agricultural systems resilient and provides the raw materials for formal breeding. Farmers in eastern Africa have developed crop landraces to grow well under local conditions or when faced with particular constraints, such as poor soils, drought or high altitude, or for specific types of food (Blum and Sullivan 1986; Asfaw 1989; Demissie and Bjørnstad 1996; Teshome et al. 1999; Kebebew et al. 2001; Tsehaye et al. 2006).

For *E. coracana* in particular, local landrace diversity is high in many regions, because formal breeding began only in the 1960s and improved varieties have not been widely adopted (Dida et al. 2008). Several studies have indicated that there is more diversity between landraces grown by a single community than there is between landraces grown in different regions (Lule et al. 2012, 2018; Manyasa et al. 2015; Gimode et al. 2016), probably because in regions where *E. coracana* is an important crop, farmers maintain a range of landraces for different uses and growth conditions. Finger millet is used for *enjera* (bread) in Ethiopia, *ugali* (stiff porridge) and *uji* (thin porridge) in Kenya and Tanzania, and beer in many regions of eastern and south-central Africa. Often these uses are specific to a particular landrace (Tsehaye et al. 2006). Additional genotypic and phenotypic variation exists in eastern African landraces because gene flow is still occurring between *E. coracana* and its wild progenitor. Wild finger millet frequently infests *E. coracana* fields, but usually flowers and sets seed earlier, which limits gene flow and minimizes mixed harvests (Dida et al. 2008). It is currently unknown when this divergence in phenology evolved, but it would have made subsequent differentiation between wild and domesticated populations much easier to achieve.

Table 1 Radiocarbon dates from later Iron Age contexts at Kakapel rock shelter

Lab code	Trench	Depth b.s. (cm)	Material type	^{14}C (years BP)	Cal. BP[a]	Note
OxA-38807	2	58	Botanical (nutshell)	845 ± 21	766–679	From feature
SUERC-86059[b]	2	80	Molar (H. sapiens)	895 ± 28	904–690	Direct date on isolated molar
WK-47410[c]	3	94	Charcoal (NID)	813 ± 15	729–677	From feature
Wk-48699[c]	3	100	Botanical (Fabaceae)	962 ± 18	914–794	From feature

[a] 95.4% probability range using mixed curve calibration (Hogg et al. 2020; Reimer et al. 2020)

[b] See Wang et al. (2020) for details on this sample

[c] Directly associated with archaeological *E. coarcana* samples

E. coracana landraces are relatively more diverse phenotypically than they are genotypically, and phenotypic characters can be used to more consistently differentiate between sub-populations from different regions (Dida et al. 2008). Heartening as this is for the archaeobotanist, most previous studies of phenotypic variation are not useful for comparison with archaeobotanical assemblages made up entirely of charred seeds. In a rare exception, Hilu and de Wet (1976a) used a subjective assessment of grain shape [triangular vs cordate (heart shaped)] to distinguish between highland and lowland races of *E. coracana*. They attempted to separate *E. coracana* into races on the basis of morphological characters, but most of them are not preserved in the archaeological record. Our goal was to explore the value of grain shape and size for distinguishing between populations of *E. coracana* across space and time.

Kakapel rock shelter

Kakapel (from Kakapeli in the Teso language) is a granitic inselberg (isolated rock hill) located at 1,420 m a.s.l. in the Chelelemuk hills in Busia county, of western Kenya (Fig. 1). Erosion has created several sheltered areas of various sizes as well as small pseudo-caves around its entire perimeter. A large rock shelter along its western side has preserved Iron Age rock-art, and this is the primary Kakapel rock shelter archaeological site. The site was first identified by O. Odak (Odak 1977, 1980), who described it as a Later Iron Age to historic period occupation based on surface scatters of Roulette decorated pottery typical of the last ca. 1,000 years around Lake Victoria, and the presence of grindstones. Kakapel is currently a protected site managed by the Trust for African Rock Art (TARA) and the National Museums of Kenya (NMK). The NMK carried out test excavations there in 2012 and expanded this work in 2015 in preparation for installing a fence to protect the rock art panel. In 2018, excavations resumed as part of collaborations between the NMK and the Max Planck Institute for the Science of Human History, Germany.

Excavations at Kakapel have so far revealed rich Later Iron Age horizons extending from ~ 30 to 110 cm below the present ground surface and containing a high density of hearths, pits and other archaeological features, but no evidence of house structures. A detailed summary of the archaeological remains is forthcoming; see also details on occupation sequence in Wang et al. (2020). In addition to association with diagnostic Roulette pottery, radiocarbon dates on material from features yielding the majority of the archaeobotanical remains recovered from the site firmly place its use in the Later Iron Age, between ca. 677 and 914 cal BP (Table 1). The ratio of northern to southern hemisphere carbon cycle influence this close to the Equator is unknown and so we used a prior uniform distribution (between 0 and 100) to express the unknown degree of mixing between the northern (IntCal20) and southern (ShCal20) radiocarbon calibration curves when calculating the calibrated ranges in Table 1 (Hogg et al. 2020; Reimer et al. 2020).

Materials and methods

We collected 136 flotation samples at Kakapel, consisting of 1,232 L of soil. Of these, 33 samples (320 L in total) have been completely analysed, while the analysis of other samples is in progress. Heavy fractions were sorted in the field and any charcoal was combined with the light fraction. In the laboratory, the light fraction was weighed to the nearest 0.01 g then sieved with 2, 1 and 0.5 mm geological sieves. All material was examined under a dissecting microscope at 10–40×. The > 2 mm sample was sorted completely into wood charcoal, nutshells, seeds, unidentifiable carbonized material and uncarbonized material. The > 1 and > 0.5 mm samples were scanned for seeds and seed fragments. So far, 397 seeds have been recovered, but only a small fraction of these have been identified beyond family. To aid identification, we obtained examples of crop seeds that may have been grown at the site from the United States Department of Agriculture Germplasm Resources Information Network (USDA GRIN), (Table 2), and consulted seed collections at the L. H. Bailey Hortorium, the East African Herbarium and the Washington University Palaeoethnobotany Laboratory. For grass seeds, we

Table 2 Provenances of accessions of modern landraces. Locations where samples were collected are labelled by laboratory number in Fig. 1

Lab. #	USDA GRIN #	Collection	Country	Locality	Year collected	Latitude	Longitude
EC02	PI 321129 01 SD	USDA	Uganda	Mugusu	1967	0.611178	30.21389
EC03	PI 273887 or SD	USDA	Ethiopia	Asmara	1961	15.31488	38.90574
EC04	PI 318898 or SD	USDA	Ethiopia	Addis Ababa	1961	9.013581	38.74904
EC08	PI 321086 01 SD	USDA	Kenya	Kimilili	1967	0.78361	34.71703
EC09	PI 248523 01 SD	USDA	DR Congo	Gutari	1958	− 11.7096	27.48552
EC10		MPISHH	Zambia	Kapiri Mposhi	2019	− 13.8847	28.67743
EC11		MPISHH	Zambia	Kapiri Mposhi	2019	− 13.8847	28.67743
EC12		MPISHH	Zambia	Kabwe	2019	− 14.4301	28.43984
EC13		WASHU	Tanzania	Pemba	2004	− 5.05161	39.78827
ECA01	PI 226270 01 SD	USDA	Zimbabwe	Salisbury	1955	− 17.8114	31.01463
ECA02	PI 315700 01 SD	USDA	South Africa	Pretoria	1966	− 25.7233	28.23983

considered other wild and cultivated taxa that may have been used at the site and consulted published images of these (Zach and Klee 2003; Klee et al. 2004; Fuller 2006; Beldados 2019). The *E. coracana* grains analysed here come from four flotation samples (43 L total) taken from Trench 3 at Kakapel. Two of the radiocarbon dates in Table 1 were drawn from the same samples as the analysed grains (729–677 and 914–794 cal BP). For this analysis, we treat all of the grains from these samples as a single Late Iron Age population.

E. coracana grains can be identified by several characteristics. They are round to heart-shaped in plan view and, unlike many other millets, are nearly spherical, as revealed by a lateral view (Fig. 2). They also have a granular grain surface texture. This granular texture is more pronounced in the wild *E. coracana* ssp. *africana*, in which granules are uniformly distributed along ridges. Seeds of the wild subspecies are of a completely different shape, being oblong in both plan and lateral views (Fig. 2). They are more easily confused with *E. indica* than with domesticated *E. coracana*, but are larger than the former (Hilu and de Wet 1976b). A total of 52 grain were identified as *E. coracana* and were complete enough to measure. We also identified two grains as *E. coracana* ssp. *africana* based on a subjective assessment of the seed shape and grain surface texture (Hilu and de Wet 1976b).

We characterized the diversity of modern and ancient landraces in terms of seed size (length, width, thickness and area) and quantitative measurements of shape (aspect ratio and roundness), features that should nearly always be preserved in complete, identifiable archaeobotanical specimens (Fig. 2). We used length, width and thickness because these are standard measurements used in the identification and analysis of grain crops in Africa (Zach and Klee 2003; Klee et al. 2004; D'Andrea 2008; Giblin and Fuller 2011). We introduce the use of area (mm^2) in addition to these standard measurements because it shows increases in size due to increasing roundness more completely than linear measurements (Mueller 2017). Just such a change is apparent between wild and domesticated *E. coracana* (Fig. 2), so area is a better single measurement than length, width and thickness for differentiating between grains of wild and domesticated plants. We also used aspect ratio (major axis/minor axis) and roundness ($4 \times [Area]/\pi \times [Major\ axis]^2$), shape descriptors that are roughly inverse and show the degree of elongation. In order to obtain these shape and size data, we took microphotographs in plan and lateral view at 120 × magnification using a Dinolite AM4815ZTL digital microscope of both ancient and modern and wild and cultivated finger millet grains and analysed the images with ImageJ v. 1.45 s.

Carbonization experiments

We conducted the experiments described below using a Thermolyne muffle furnace, which we preheated in all experiments before grains were put in it. We used grains from accession EC11 (Table 2) and buried them under ~ 1 cm of quartz sand in ceramic crucibles.

We undertook a series of exploratory experiments to identify the range of temperatures and duration of exposure to heat under which *E. coracana* would be fully carbonized without damage to the grain (Table 3). Experimental carbonization of *E. coracana* has previously only been attempted by Hilu et al (1979, p. 330), who did not specify sample size, temperature or duration for their experiment. They reported a "slight increase in size and occasional cracking of the seed coat" after carbonization, but no measurements for either of these observations. Based on our own experiments, we suspect that they heated their grains quickly to a temperature above 220 °C, since this leads to distortion by puffing and popping, which may slightly increase grain size in the rare specimens where it does not also fracture the caryopsis coat, rendering size and shape unmeasurable. Seeds that are cracked and puffed are less likely to survive hundreds of years of taphonomic processes, as well as the processes of excavation and flotation, and are often unidentifiable even if they are recovered because they lack diagnostic features. Incompletely carbonized seeds

Table 3 Exploratory carbonization experiments undertaken to determine the range of temperatures and duration of exposure to heat that would result in complete carbonization and good preservation of *E. coracana* grains

Temperature (°C)	Duration (min)	Sample size	Result
275	30	20	20/20 completely carbonized; 20/20 caryopsis coats cracked and seeds puffed
180	120	20	0/20 seeds carbonized beyond caryopsis coat; 0/20 caryopsis coats cracked
225	75	20	9/20 incompletely carbonized; 16/20 caryopsis coats cracked and seeds puffed
200	180	20	0/20 carbonized beyond caryopsis coat; 0/20 caryopsis coats cracked
215	180	20	20/20 fully carbonized, 2/20 caryopsis coats cracked and seeds puffed

Table 4 Results of the main carbonization experiment in which changes in shape and size of *E. coracana* grains were measured after 3 h at 215 °C

Measurement	Mean	SD	Mean post-carbonization	SD	P (≠0)	Correction factor
E. coracana (n = 100)						
Area (mm^2)	2.04	0.295	1.80	0.334	<0.0001	1.13
Length (mm)	1.59	0.137	1.51	0.130	<0.0001	1.05
Width (mm)	1.65	0.183	1.55	0.163	<0.0003	1.06
Thickness (mm)	1.39	0.082	1.32	0.082	0.0148	1.05
Aspect ratio	1.11	0.083	1.11	0.089	0.7141	–
Roundness	0.91	0.064	0.90	0.067	0.5826	–
E. coracana ssp. *africana* (n = 40)						
Area (mm^2)	0.91	0.109	0.87	0.105	0.0992	–
Length (mm)	1.49	0.127	1.40	0.133	0.0046	1.06
Width (mm)	0.82	0.071	0.83	0.069	0.2264	–
Thickness (mm)	0.89	0.069	0.87	0.059	0.2160	–
Aspect ratio	1.91	0.260	1.79	0.250	0.0460	1.06
Roundness	0.53	0.070	0.57	0.077	0.0370	0.93

See Fig. 2 for length, width and thickness measurements. Area and shape descriptors measured from ventral view. Area = mm^2; Aspect ratio = (major axis/minor axis); roundness = $4 \times [Area]/\pi \times [Major\ axis]^2$

will decompose in most environments. Therefore, the range of temperatures and durations of exposure to heat that will carbonize but not significantly distort or destroy seeds is of interest (Märkle and Rösch 2008).

After determining that a treatment of 215 °C for 3 h would result in well-preserved, completely carbonized seeds, we did a larger experiment to determine how carbonization affects seed size and shape. We took microphotographs of 100 *E. coracana* seeds in batches of ten in plan (ventral orientation, Fig. 2) and lateral views at ×120 magnification (Fig. 2), buried them in sand in ten separate ceramic crucibles and placed them in the furnace for 3 h at 215 °C. After they were cool, we extracted the grains, discarded any with fractured caryopses coats and photographed them again. We measured the images from before and after charring using ImageJ, compared sample means and calculated average differences per batch to determine if the shapes and sizes changed in predictable ways as a result of charring. We repeated the same experiment with a smaller sample of *E. coracana* ssp. *africana*, n = 40. We only measured change in grain thickness for a smaller sample of 40 *E. coracana* and 40 *E. coracana* ssp. *africana*, since it required a second set of microphotographs in lateral view.

Morphometric analysis

We applied the correction factors for charring in Table 4 to the archaeobotanical specimens from Kakapel. Correction factors are discussed in the Results section. Our modern comparative collection was assembled from accessions housed in USDA GRIN, collections made by Goldstein (MPI SHH) and a collection made by S. Walshaw (Wash U). The latter two sources are grains that were grown in their countries of origin by local farmers, while the USDA GRIN material came from plants grown at the Plant Genetic Resources Conservation Unit at Griffin, Georgia, from lineages originally collected in the 1950s and 1960s in eastern Africa (Fig. 1; Table 2).

These differences in the origins of the grains may affect seed morphology due to their developmental responses to climate, soil conditions and cultivation techniques, as well as genetic differences between landraces. We measured random subsamples of 20 grains of each accession for a total comparative sample of 180. We measured the grains from two accessions of *E. coracana* ssp. *africana* obtained from the USDA, for a total sample of 40. We also included in our analysis measurements of seed length, width and thickness of three ancient *E. coracana* assemblages from Rwanda (Fig. 1; Giblin and Fuller 2011). We corrected Giblin and Fuller's (2011 *Supplemental Materials*) measurements from carbonized caryopses using the correction factors developed in this study, and used the original measurements for the mineralized seeds. We used area as a single measurement of size to compare the Kakapel assemblage to modern *E. coracana* accessions, but used linear measurements to compare the Kakapel assemblage with those reported by Giblin and Fuller (2011), who did not report area.

Results

Carbonization experiment

Our exploratory experiments showed that *E. coracana* is unlikely to be preserved if it is carbonized at temperatures above 220 °C because these temperatures cause the caryopsis coat to crack and fall away, distorting the shape of the seed. At or below 200 °C, *E. coracana* does not carbonize beyond the caryopsis coat after 3 h, our longest experiment. It would require a yet to be determined duration of exposure to heat in order to fully carbonize finger millet seeds at these low temperatures. The sensitivity of *E. coracana* to high temperatures may partially explain its rarity in the archaeological record. For comparison, after 3 h of exposure to heat in reducing conditions, as in our experiment, *Setaria italica* (foxtail millet) carbonizes and preserves well between 225 and 450 °C and *Panicum miliaceum* (broomcorn millet) has a smaller temperature range of 275–375° (Märkle and Rösch 2008), while caryopses of *Triticum* and *Hordeum* will be preserved between 250 and 450 °C (Boardman and Jones 1990). *E. coracana* grains would be destroyed by a large range of medium to high temperature fires that would lead to good preservation of these other taxa.

Seeds showing carbonization without cracking of the caryopsis coat and puffing of the grain varied from 10/10 to 8/10 per batch, resulting in 91/100 measurable *E. coracana* caryopses after carbonization and 40/40 *E. coracana* ssp. *africana* caryopses. The diagnostic texture of the caryopsis coat was universally well preserved in our experiment (Fig. 2). Changes in seed shape and size due to carbonization are reported in Table 4 and are slight overall. We list correction factors (mean of uncarbonized measurement/mean of carbonized measurement) if the percentage change due to carbonization was in the same direction (positive or negative) in all batches, and if the mean for the carbonized sample was significantly different ($p < 0.05$ in a two-tailed t test) from that of the uncarbonized sample. *E. coracana* grains did not change shape (aspect ratio or roundness) in a predictable manner or to a significant degree because they decreased in size to roughly to the same extent in all three measured dimensions (length, width and thickness). Grain length, width, thickness and area in plan view all decreased slightly after carbonization (Table 4). We suggest that to correct for the effects of carbonization, analysts multiply measurements of carbonized archaeobotanical specimens by 1.05 for length and thickness, by 1.06 for width and by 1.13 for area measurements. Wild finger millet seeds also shrank due to carbonization in terms of area and length, while changes in width and thickness were not significant, resulting in an overall decrease in aspect ratio and increase in roundness (Table 4). We suggest correction factors of × 1.06 for length and aspect ratio, and × 0.93 for roundness for carbonized wild finger millet seeds when compared to uncarbonized modern specimens.

Morphometric analysis

The Kakapel *E. coracana* was significantly smaller than all of the modern populations (Student's t test, $p < 0.0004$ for all comparisons). It was most similar to EC04, an accession from Ethiopia that was also significantly smaller than all other populations (Table 5). In order to include the measured Iron Age assemblages from Rwanda in the comparison, we conducted the same test with length × width as an overall measure of size (Fig. 3). The Iron Age *E. coracana* from Musanze II, Nguri cave and Karama are larger than the Kakapel examples, but still significantly smaller than all modern landraces other than EC04. The archaeobotanical exception is the assemblage from Musanze III ($n = 6$), whose average size is the largest of any assemblage, modern or ancient (Fig. 3; Table 5) and similar in size to large-grained modern landraces from Tanzania (EC13) and Uganda (EC02). Except Musanze III, the three other archaeological assemblages from Rwanda are not significantly different from each other in terms of grain size, and all are significantly larger than those from Kakapel (Fig. 3; Student's t test, $p < 0.05$ for all comparisons).

The Kakapel assemblage is larger grained (but not significantly) than the two accessions of wild *E. coracana* that we measured, in terms of both area and length × width. In terms of shape, the Kakapel assemblage is similar to most of the modern landraces that we measured, having an average aspect ratio of 1.09, near the overall mean 1.08 (Fig. 4). Wild and domesticated *E. coracana* are significantly different in terms of both shape and size. The aspect ratio of wild *E. coracana* is higher than that of domesticated *E. coracana* with more elongated and smaller grains (Table 5). The Kakapel assemblage has an intermediate morphology in that it is small-grained, but

Table 5 Results of the morphometric analysis of the modern comparative collection and Iron Age archaeobotanical assemblages

Population	*n*	Area (mm^2)		Length (mm)		Width (mm)		Thickness (mm)		Aspect Ratio		Roundness	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Eleusine coracana													
EC02	20	2.19	0.346	1.68	0.120	1.73	0.174	1.30	0.114	1.08	0.066	0.93	0.055
EC03	20	1.86	0.221	1.59	0.078	1.53	0.114	1.48	0.085	1.05	0.032	0.95	0.027
EC04	20	1.45	0.217	1.40	0.108	1.37	0.099	1.43	0.083	1.05	0.027	0.95	0.024
EC08	20	1.77	0.339	1.50	0.153	1.56	0.147	1.32	0.140	1.09	0.046	0.92	0.040
EC09	20	1.89	0.329	1.57	0.125	1.57	0.174	1.32	0.087	1.06	0.034	0.94	0.030
EC10	20	1.84	0.441	1.54	0.190	1.54	0.194	1.30	0.109	1.07	0.043	0.93	0.035
EC11	20	2.10	0.191	1.63	0.098	1.69	0.099	1.39	0.082	1.10	0.059	0.91	0.047
EC12	20	1.89	0.329	1.56	0.130	1.57	0.147	1.31	0.132	1.08	0.051	0.93	0.042
EC13	20	2.25	0.440	1.65	0.166	1.76	0.207	1.41	0.167	1.14	0.092	0.88	0.066
KPL C0.3	5	1.52	0.454	1.35	0.231	1.44	0.226	1.14	0.140	1.13	0.076	0.89	0.060
KPL C1.2	4	0.831	0.243	1.01	0.133	1.05	0.177	0.93	0.102	1.07	0.033	0.93	0.029
KPL C2	41	1.09	0.419	1.16	0.237	1.18	0.234	0.99	0.176	1.09	0.055	0.92	0.0457
Musanze II	7			1.39	0.176	1.32	0.224	1.34	0.194				
Musanze III	6			1.77	0.281	1.76	0.130	1.56	0.242				
Nguri Cave	5			1.52	0.118	1.45	0.163	1.41	0.188				
Karama				1.16	0.021	1.59	0.035	1.21	0.057				
E. coracana ssp. *africana*													
ECA01	20	0.94	0.062	1.44	0.137	0.86	0.056	0.92	0.058	1.74	0.133	0.58	0.047
ECA02	20	0.88	0.137	1.55	0.156	0.78	0.064	0.86	0.067	2.07	0.253	0.49	0.064
KPL C2	2	0.85	–	1.22	–	0.68	–	0.82	–	1.45	–	0.68	–

See Fig. 2 for length, width and thickness measurements. Area and shape descriptors measured from ventral view. Area = mm^2; Aspect ratio (major axis/minor axis); roundness = $4 \times [Area]/\pi \times [Major\ axis]^2$

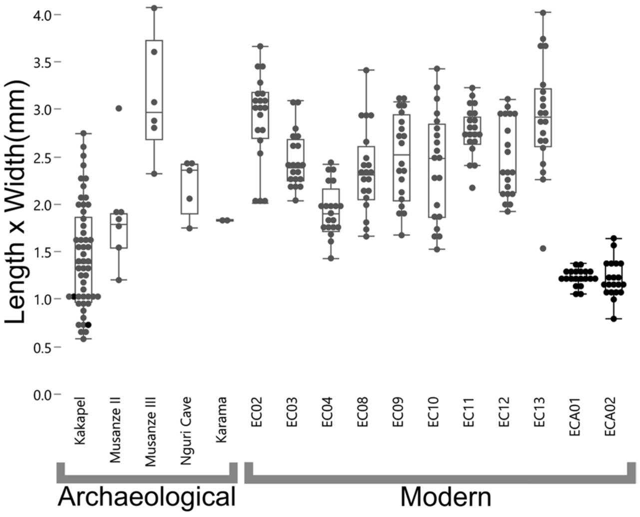

Fig. 3 Seed size (length × width) for modern comparative material and corrected archaeobotanical assemblages. The wild progenitor of *E. coracana* is represented by black dots and box plots. Comparative collection sources can be found in Table 2, measurements for Muzanze II and III, Nguri Cave and Karama from Giblin and Fuller (2011). Boxes represent median and 1st–3rd interquartile range, whiskers = 1st/3rd quartile ± 1.5 × interquartile range

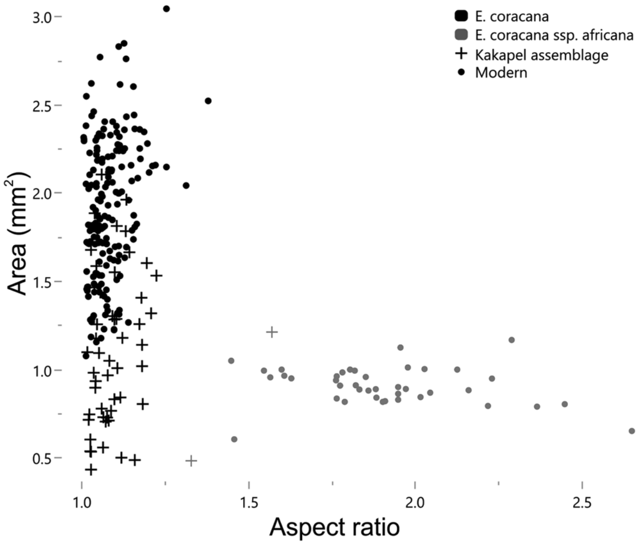

Fig. 4 Kakapel *E. coracana* seed area and aspect ratios compared to modern material. Domesticated grains are easily distinguished by aspect ratio despite their small size. Kakapel *E. coracana*, even after correction for carbonization, is significantly smaller grained than *E. coracana* landraces

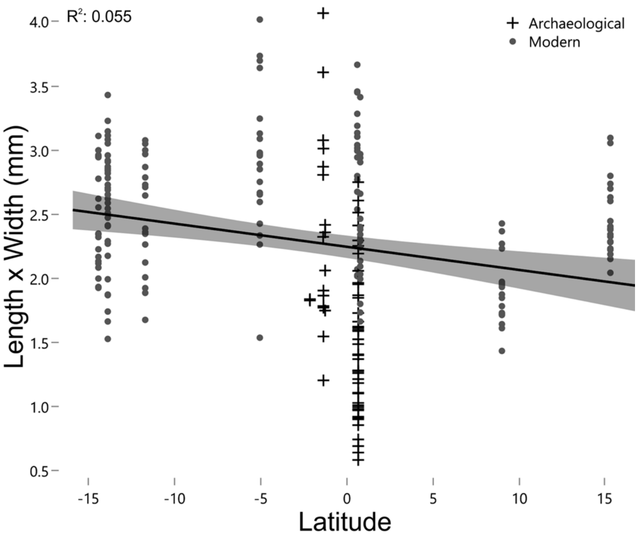

Fig. 5 Correlation between seed size and latitude for modern comparative and archaeobotanical assemblages

is easily identified as domesticated *E. coracana* both qualitatively, by caryopsis coat texture and subjective assessment of shape (Fig. 2), and quantitatively using aspect ratio (Fig. 4). The two archaeobotanical grains subjectively identified as wild *E. coracana* also have a high aspect ratio and small size compared to domesticated *E. coracana*, although their shape and size is somewhat unusual in comparison to the modern samples (Fig. 4, grey crosses). This could be an artefact of small sample size, or due to local variation in wild *E. coracana*, given that both of our comparative populations come from southern Africa (Fig. 1).

We also wanted to know if there was any relationship between grain size or shape and latitude, since *E. coracana* was probably domesticated somewhere between ~ 15° and −5° latitude and then spread south. We found that smaller caryopsis size (length × width) and higher latitude are weakly correlated for all measured domesticated *E. coracana* assemblages ($R^2 = 0.06$, Fig. 5). While aspect ratio does not seem to be a particularly sensitive measurement for distinguishing between the landraces that we measured, the Ethiopian accessions both had unusually low aspect ratios, and the material from the island of Pemba, Tanzania, had a significantly higher aspect ratio than all other accessions ($p < 0.0098$ for all comparisons) (Table 5).

Conclusions and directions for future research

Our results support previous observations about the variability of *E. coracana* and provide a basis for the analysis of archaeobotanical assemblages of this crop. We observed, for example, considerable difference in grain size between landraces collected from the same community (EC10 and EC11) and little spatial patterning in shape or size, suggesting that greater variability may be found between different landraces at a local level than between regions (Figs. 3, 5; Table 5), as indicated by previous research (Manyasa et al. 2015). Detailed ethnobotanical data are rarely available for USDA GRIN accessions, so we could not investigate the possibility that grain size or shape was associated with a particular use, such as for brewing beer or baking bread. This is an important direction for future research that might allow a more detailed interpretation of crop use in the past, or even suggest for what purpose *E. coracana* was initially domesticated.

Although there are not many archaeobotanical assemblages for comparison, it is apparent that there was diversity in *E. coracana* landraces on small temporal and spatial scales in the past, as well. All of the archaeobotanical assemblages analysed date to the same (at most) 800 year period, from 1,400 to 600 years ago (Table 1; Giblin and Fuller 2011, Table 2), and three out of the four come from northern Rwanda, yet they exhibit considerable variability in seed size (Fig. 3). The Kakapel assemblage stands out for its small seed size, but is similar in this respect to some extant landraces, such as EC04, an accession collected in a market in Addis Ababa in 1966. Although the Kakapel *E. coracana* are small, they are easily distinguished from those of their wild progenitor by their shape (measured by aspect ratio; Fig. 5) and caryopsis coat texture (Fig. 2). Both wild and domesticated *E. coracana* were recovered from Iron Age contexts at Kakapel, which shows that, then as now, wild *E. coracana* grew at the site and/or in the millet fields. While two wild-type seeds are scant evidence, their appearance in the same contexts as domesticated ones suggests that the phenological divergence in ripening time between crop and its progenitor that is evident today may not yet have evolved 1,000 years ago.

Large, well-preserved assemblages of *E. coracana* are rare, even at sites where other plant materials are abundant and archaeobotanical sampling was thorough (Young and Thompson 1999; Boardman 2000; Crowther et al. 2016). Our carbonization experiments suggest an explanation for this: compared to other cereals, *E. coracana* has a relatively small range of temperatures at which it will be well preserved by carbonization (Table 3; Boardman and Jones 1990; Märkle and Rösch 2008). These experiments unfortunately demonstrate that evidence from macrobotanical remains for *E. coracana* domestication and farming will be difficult to recover, and remains will often be fragmentary and/or fragile. For example, from the same contexts analysed for this study, we recovered an additional 32 *E. coracana* seeds that were not complete enough to measure, 59 tentatively identified as *E. coracana* on the basis of surface texture and/or shape, and 246 unidentifiable seed fragments. It is likely this preservation bias has caused archaeologists to underestimate the importance of *E. coracana* to past societies. It is also possible that the paradox of *E. coracana* appearing more frequently and earlier in India than in eastern Africa can be explained by preservation bias. If processing and/or cooking methods differed considerably between these two regions, there may simply have been more situations providing the narrow range of conditions for preservation of this crop in India than in its region of origin.

Because *E. coracana* is not easily preserved by carbonization, extraordinary care should be taken with all stages of collection and processing of flotation samples that may contain evidence of this crop. Flotation samples should be removed in chunks, not scraped, and gently processed by hand without the use of metal sieves or screens except to collect the heavy fraction. Light fractions should be stored and transported in rigid containers. All of these measures may help preserve rare and fragmentary remains until they reach the microscope. Given the preservation biases which act against the recovery of *E. coracana* seeds, microbotanical comparative collections for this crop (starch, pollen, phytoliths) are needed, and appropriate sampling for these classes of evidence at sites that might yield evidence of *E. coracana* domestication or farming should be done alongside flotation.

This study presents a preliminary morphometric dataset of modern *E. coracana* landraces that can be compared to archaeobotanical remains directly using the carbonization correction factors that we suggest (Table 4). However, given the phenotypic variability of this crop, it would be useful to expand this comparative dataset significantly using accessions for which detailed ethnobotanical data are available. This would allow an investigation of differences in grain morphology between landraces that are cultivated for different culinary uses by the same community, or those that are adapted to particular environmental conditions—both of which could facilitate a more detailed interpretation of ancient *E. coracana* farming and food culture. While the process and timing of *E. coracana* domestication remain mysterious, the Kakapel assemblage represents a useful ancient population of finger millet that could help bridge the evolutionary gap between modern landraces and wild populations as more archaeobotanical evidence comes to light.

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Data availability Source data is available upon request from the corresponding author.

Declarations

Conflict of interest The authors declare no conflicts of interest or competing interests.

References

Ambrose SH, Collett D, Collett D, Marshall F (1984) Excavations at Deloraine, Rongai, 1978. Azania 19:79–104

Asfaw Z (1989) Relationships between spike morphology, hordeins and altitude within Ethiopian barley, *Hordeum vulgare* L. (Poaceae). Hereditas 110:203–209

Barron A, Fuller DQ, Stevens C, Champion L, Winchell F, Denham T (2020) Snapshots in time: MicroCT scanning of pottery sherds determines early domestication of sorghum (*Sorghum bicolor*) in East Africa. J Archaeol Sci 123:105259. https://doi.org/10.1016/j.jas.2020.105259

Beldados A (2016) Paleoethnobotanical study of ancient food crops and the environmental context in North-East Africa, 6000 BC-AD 200/300. (Cambridge Monographs in African Archaeology 88, BAR International Series 2206). BAR Publishing, Oxford

Beldados A (2019) Millets in eastern Sudan: an archaeobotanical study. Azania 54:501–515. https://doi.org/10.1080/0067270X.2019.1691844

Belton PS, Taylor JRN (2004) Sorghum and millets: protein sources for Africa. Trends Food Sci Technol 15:94–98. https://doi.org/10.1016/j.tifs.2003.09.002

Bisht M, Mukai Y (2001) Genomic *in situ* hybridization identifies genome donor of finger millet (*Eleusine coracana*). Theor Appl Genet 102:825–832

Blum A, Sullivan CY (1986) The comparative drought resistance of landraces of sorghum and millet from dry and humid regions. Ann Bot 57:835–846

Boardman S (2000) Archaeobotany. In: Philipson DW (ed) Archaeology of Aksum, Ehtiopia, 1993–7, vol 2. British Institute in Eastern Africa, London, pp 363–368

Boardman S, Jones G (1990) Experiments on the effects of charring on cereal plant components. J Archaeol Sci 17:1–11

Boivin N, Fuller DQ (2009) Shell middens, ships and seeds: exploring coastal subsistence, maritime trade and the dispersal of domesticates in and around the ancient Arabian Peninsula. J World Prehist 22:113–180

Boivin N, Crowther A, Prendergast M, Fuller DQ (2014) Indian Ocean food globalisation and Africa. Afr Archaeol Rev 31:547–581

Crowther A, Lucas L, Helm R et al (2016) Ancient crops provide first archaeological signature of the westward Austronesian expansion. Proc Natl Acad Sci USA 113:6,635–6,640

Crowther A, Prendergast ME, Fuller DQ, Boivin N (2018) Subsistence mosaics, forager-farmer interactions, and the transition to food production in eastern Africa. Quat Int 489:101–120

D'Andrea AC (2008) T'ef (*Eragrostis tef*) in ancient agricultural systems of highland Ethiopia. Econ Bot 62:547–566

Demissie A, Bjørnstad Å (1996) Phenotypic diversity of Ethiopian barleys in relation to geographical regions, altitudinal range, and agro-ecological zones: as an aid to germplasm collection and conservation strategy. Hereditas 124:17–29

Dida MM, Ramakrishnan S, Bennetzen JL, Gale MD, Devos KM (2007) The genetic map of finger millet, *Eleusine coracana*. Theor Appl Genet 114:321–332

Dida MM, Wanyera N, Dunn MLH, Bennetzen JL, Devos KM (2008) Population structure and diversity in finger millet (*Eleusine coracana*) germplasm. Tropical Plant Biol 1:131–141

Esau K (1965) Plant anatomy, 2nd edn. Wiley, New York

Fuller DQ (2006) Agricultural origins and frontiers in South Asia: a working synthesis. J World Prehist 20:1–86

Giblin JD, Fuller DQ (2011) First and second millennium A.D. agriculture in Rwanda: archaeobotanical finds and radiocarbon dates from seven sites. Veget Hist Archaeobot 20:253–265

Gimode D, Odeny DA, de Villiers EP et al (2016) Identification of SNP and SSR markers in finger millet using next generation sequencing technologies. PLoS ONE 11:e0159437

Gowlett JAJ, Hedges REM, Law IA, Perry C (1987) Radiocarbon dates from the Oxford AMS System: archaeometry datelist 5. Archaeometry 29:125–155

Gupta SM, Arora S, Mirza N et al (2017) Finger Millet: a "certain" crop for an "uncertain" future and a solution to food insecurity and hidden hunger under stressful environments. Front Plant Sci 8:643. https://doi.org/10.3389/fpls.2017.00643

Harlan JR (1971) Agricultural origins: centers and noncenters. Science 174:468–474

Hilu KW, de Wet JMJ (1976a) Racial evolution in *Eleusine coracana* ssp. *coracana* (finger millet). Am J Bot 63:1,311–1,318

Hilu KW, de Wet JMJ (1976b) Domestication of *Eleusine coracana*. Econ Bot 30:199–208

Hilu KW, Johnson JL (1992) Ribosomal DNA variation in finger millet and wild species of *Eleusine* (Poaceae). Theor Appl Genet 83:895–902

Hilu KW, de Wet JMJ, Harlan JR (1979) Archaeobotanical studies of *Eleusine coracana* ssp. *coracana* (finger millet). Am J Bot 66:330–333

Hogg AG, Heaton TJ, Hua Q et al (2020) SHCal20 Southern Hemisphere calibration, 0–55,000 years cal BP. Radiocarbon 62(4):759–778

Kebebew F, Tsehaye Y, McNeilly T (2001) Morphological and farmers cognitive diversity of barley (*Hordeum vulgare* L.[Poaceae]) at Bale and North Shewa of Ethiopia. Genet Resour Crop Evol 48:467–481

Klee M, Zach B, Neumann K (2000) Four thousand years of plant exploitation in the Chad Basin of northeast Nigeria I: the archaeobotany of Kursakata. Veget Hist Archaeobot 9:223–237

Klee M, Zach B, Stika H-P (2004) Four thousand years of plant exploitation in the Lake Chad Basin (Nigeria), part III: plant impressions in potsherds from the Final Stone Age Gajiganna Culture. Veget Hist Archaeobot 13:131–142

Lange G (1991) Appendix V: a seed of wild finger millet from Gogo Falls. In: (Robertshaw P) Gogo Falls: excavations at a complex archaeological site east of Lake Victoria. Azania 26:191–192

Lavé J, Wenger E (1991) Situated learning: Legitimate peripheral participation. Cambridge University Press, Cambridge

Lule D, Tesfaye K, Fetene M, de Villiers S (2012) Multivariate analysis for quantitative traits in finger millet (*Eleusine coracana* subsp. *coracana*) population collected from eastern and southeastern Africa: detection for patterns of genetic diversity. Int J Agric Res 7:303–314

Lule D, de Villiers S, Fetene M, Odeny DA, Rathore A, Das RR, Tesfaye K (2018) Genetic diversity and association mapping of Ethiopian and exotic finger millet accessions. Crop Pasture Sci 69:879–891

Manning K, Pelling R, Higham T, Schwenniger J-L, Fuller DQ (2011) 4500-year old domesticated pearl millet (*Pennisetum glaucum*) from the Tilemsi Valley, Mali: new insights into an alternative cereal domestication pathway. J Archaeol Sci 38:312–322

Manyasa EO, Tongoona P, Shanahan P, Mgonja MA, de Villiers S (2015) Genetic diversity in East African finger millet (*Eleusine coracana* (L.) Gaertn) landraces based on SSR markers and some qualitative traits. Plant Genet Resour 13:45–55

Märkle T, Rösch M (2008) Experiments on the effects of carbonization on some cultivated plant seeds. Veget Hist Archaeobot 17:257–263

Mueller NG (2017) Carbonization, differential preservation, and sampling bias in domestication studies: an erect knotweed (*Polygonum erectum* L.) case study. J Archaeol Sci Rep 13:303–311

Murray SS (2004) Searching for the origins of African rice domestication. Antiquity 78:1–3

Nazarea VD (2005) Heirloom seeds and their keepers: marginality and memory in the conservation of biological diversity. University of Arizona Press, Tuscon

Odak O (1977) Kakapeli and other recently discovered rock paintings in the Western Highlands of Kenya. Azania 12:187–192

Odak O (1980) Recent fieldwork in west Kenya. Nyame Akuma 16:10–14

Pautasso M, Aistara G, Barnaud A et al (2013) Seed exchange networks for agrobiodiversity conservation: a review. Agron Sustain Dev 33:151–175

Phillipson DW (1977) The excavation of Gobedra rock-shelter, Axum: an early occurrence of cultivated finger millet in northern Ethiopia. Azania 12:53–82

Phillipson DW (2000) The Appendix VI. In: Phillipson DW (ed) The archaeology at Aksum, Ethiopia, 1993–7, vol 2. The British Institute of Eastern Africa, London, pp 504–506

Prendergast ME, Lipson M, Sawchuk EA et al (2019) Ancient DNA reveals a multistep spread of the first herders into sub-Saharan Africa. Science 365:eaaw6275

Reimer PJ, Austin WEN, Bard E et al (2020) The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). Radiocarbon 62:725–757. https://doi.org/10.1017/RDC.2020.41

Robertshaw P (1991) Gogo falls: excavations at a complex archaeological site east of Lake Victoria. Azania 26:63–195

Teshome A, Fahrig L, Torrance JK, Lambert JD, Arnason TJ, Baum BR (1999) Maintenance of sorghum (*Sorghum bicolor*, Poaceae) landrace diversity by farmers' selection in Ethiopia. Econ Bot 53:79–88

Tropicos (2020) Tropicos org. Missouri Botanical Garden. https://tropicos.org. Accessed Oct 2020

Tsehaye Y, Berg T, Tsegaye B, Tanto T (2006) Farmers' management of finger millet (*Eleusine coracana* L.) diversity in Tigray, Ethiopia and implications for on-farm conservation. Biodivers Conserv 15:4,289–4,308

Walshaw SC (2010) Converting to rice: urbanization, Islamization and crops on Pemba Island, Tanzania, AD 700–1500. World Archaeol 42:137–154. https://doi.org/10.1080/00438240903430399

Wang K, Goldstein S, Bleasdale M et al (2020) Ancient genomes reveal complex patterns of population movement, interaction, and replacement in sub-Saharan Africa. Sci Adv 6:eaaz0183

Winchell F, Stevens CJ, Murphy C, Champion L, Fuller DQ (2017) Evidence for sorghum domestication in fourth millennium BC eastern Sudan: spikelet morphology from ceramic impressions of the Butana Group. Curr Anthropol 58:673–683

Wright PJ (2003) Preservation or destruction of plant remains by carbonization? J Archaeol Sci 30:577–583. https://doi.org/10.1016/S0305-4403(02)00203-0

Wright PJ (2008) Understanding the carbonization and preservation of sunflower and sumpweed remains. MidCont J Archaeol 33:139–153

Young R, Thompson G (1999) Missing plant foods? Where is the archaeobotanical evidence for sorghum and finger millet in East Africa? In: van der Veen M (ed) The exploitation of plant resources in Ancient Africa. Kluwer Academic/Plenum Publishers, New York, pp 63–72

Zach B, Klee M (2003) Four thousand years of plant exploitation in the Chad Basin of NE Nigeria II: discussion on the morphology of caryopses of domesticated *Pennisetum* and complete catalogue of the fruits and seeds of Kursakata. Veget Hist Archaeobot 12:187–204

Zhang H, Hall N, Goertzen LR, Chen CY, Peatman E, Patel J, McElroy JS (2019) Transcriptome analysis reveals unique relationships among *Eleusine* species and heritage of *Eleusine coracana*. Genes Genomes Genet 9:2,029–2,036

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