



# Sorghum Domestication and Diversification: A Current Archaeobotanical Perspective

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**Abstract.** *Sorghum bicolor*, one of the world's five most important crops, originated in Africa. While this has long been clear, accumulating data from both archaeobotany and genetics, provides the basis for a new overview on the domestication process, racial evolution, and geographical dispersal of sorghum. Archaeobotanical finds from 113 sites in Africa and Eurasia are reviewed and mapped. Of these only 16 provide identifications of probable morphological races. Domestication is evidently taking place more than 3000 years BC in the eastern Sudan near the Atbara and Gash rivers. Early domesticated race bicolor then spread to South Asia around 2000 BC and to the Niger Basin in West Africa after 1000 BC. The framework of five cultivated races remains useful, with the original domesticated race bicolor being characterized by tight-fitting hulls requiring dehusking and the other races representing subsequent parallel evolution for free-threshing and larger-grained cultivars. This took place at least three times, including race 'caudatum' focused initially on the Sahelian region race 'durra' that evolved probably in India, and race 'guinea' that evolved in forested West Africa. Early race guinea in turn produced an even more forest adapted 'mageritiferrum' type that appears to be ancestral to southern African guinea and 'kafir' sorghums, implying a dispersal across the central African rainforests. In contrast other eastern African caudatums and 'bicolor' types presumably followed a savannah dispersal. In addition to the early dispersal of race bicolor from Africa to India, which was ancestral to East Asian sorghums, a later dispersal of guinea types is inferred to have taken place from southeastern Africa across the Indian Ocean.

**Keywords:** Archaeology · Genetics · Races · Nubia · India

## Introduction

Alongside wheat, barley, maize and rice, sorghum forms one of the five dominant staple cereal crops, and with pearl millet is one of the two main cereal crops to emerge from Africa. For much of Africa, the history of sorghum is the history of early farming. Yet despite its significance it is the only one of the five major cereals whose domestication is still relatively little understood in terms of the timing, location(s) of domestication, ecological environment, and the nature and length of this process.

Some 40 years ago Harlan and Stemler (1976) wrote a seminal paper "The races of Sorghum in Africa", and together with "Variability in *Sorghum bicolor*" (de Wet et al. 1976), formed an important step in our understanding of sorghum domestication.

Here, we revisit these papers presenting an update of the current state of knowledge, utilizing a database of archaeobotanical finds across Africa and Eurasia alongside recent insights from molecular genetics. After summarizing the variability of sorghum and genetic evidence for the relationships between different morphological and geographical populations we summarize the archaeobotanical evidence. We summarize new evidence for early cultivation and the domestication process in eastern Sudan, followed by a review of the chronology of the spread of sorghum across Africa and Asia, and the evidence for the evolution and dispersal of advanced free-threshing races of sorghum.

One of the challenges to documenting the cultural and evolutionary history of sorghum is a paucity of hard evidence in terms of archaeobotanical remains. Undoubtedly the biggest contributor to this problem has been the limited application of large scale and systematic archaeobotanical sampling programs in Africa, although these are now becoming increasingly common, with important results (e.g. Bigga and Kahlheber 2011; Giblin and Fuller 2011; Logan 2012; Crowther et al. 2016). Nevertheless, preservation on African sites is often poor, which is likely exacerbated by both patterns of occupational mobility associated with the importance of pastoralism as well as high bioturbation in tropical soils. One important line of evidence has proved to be the impressions in ceramics from the use from plant harvesting or processing waste as temper (e.g. Stemler 1990; Manning and Fuller 2014; McClatchie and Fuller 2014; Beldados et al. 2018; Winchell et al. 2017). Such studies of ceramic plant fossils offers a method by which to gain some plant evidence from even the most deflated pastoral sites and can be studied from existing archives of ceramics of excavations or surveys in regions that may be less accessible to modern re-sampling.

## The State of Knowledge 40 Years Ago

Research into the domestication of sorghum prior to the late 1960's had undoubtedly been hampered by complications within the taxonomy of the species. The first significant attempt to decipher the cultivated sorghums was made by Dr Otto Stapf (1917), an Austrian born botanist and pioneer of archaeobotany (Stapf 1886), during his time at the Royal Botanical Gardens in Kew. However, it was soon clear on the completion of this work that further inquiry was needed and to this effect Hugh Charles Sampson, Kew's first economic botanist, wrote to various Directors of Agriculture across the former British Empire requesting flowering and fruiting sorghum specimens that were sent to Kew (see Hill, in Snowden 1936, p. iii). The task to classify this material was handed to Joseph Davenport Snowden a recently retired economic botanist within the Department of Agriculture in Uganda. The culmination of this work was the "*Cultivated Races of Sorghum*" (Snowden 1936) a meticulously detailed work that divided cultivated sorghums into 6 sub-series, comprising 28 cultivated species, and 156 varieties.

This work was later revised and simplified by Harlan and de Wet (1972) into five basic cultivated races and 10 intermediate races, based upon their seeds, glumes and inflorescence shape (see Table 1). The taxonomy outlined by Harlan and colleagues (Harlan and de Wet 1972; de Wet et al. 1976; Harlan and Stemler 1976) also proposed

that wild, weedy and cultivated sorghums were treated as a single species, *Sorghum bicolor*, with five races of the domesticated subspecies *bicolor*, and four African wild races in the subspecies *arundinaceum* (now subsp. *verticilliflorum*). A wild sorghum, currently *Sorghum propinquum* (Kunth) Hitchc. was also classified as a separate race, but was noted to be the only race found outside Africa (de Wet et al. 1976). In Table 2 we provide a simplified comparison of a binomial taxonomy, in which wild forms and domesticated forms are kept as separate species (a simpler system to follow archaeobotanically), and the single species taxonomy de Wet (1977), updated by Wiersema and Dahlberg (2007). In this paper we will follow the binomial system.<sup>1</sup>

The domestication of sorghum was proposed by Harlan and Stemler (1976) to have occurred in the savannah between western Ethiopia and eastern Chad, e.g. in the Republic of the Sudan from subsp. *arundinaceum* (correctly subsp. *verticilliflorum* (Steud.) de Wet ex Wiersema and Dahlberg 2007), presumably from the wild race *aethiopicum*, which is adapted to drier semi-desert/Sahel conditions. The oldest race they identified as *bicolor* on the basis of it being the least morphologically specialized, having the widest geographical distribution, its similarities to *arundinaceum* and that back-crossing the other races with wild sorghums resulted in hybrids displaying many of the *bicolor* characteristics (see de Wet et al. 1976).

The other four races are characterized by being free-threshing, in contrast to the tightly hulled grains of *S. arundinaceum* or race *bicolor*. Thus sorghum evolution parallels wheat and barley in the post-domestication selection for free-threshing forms (see Zohary et al. 2012; Fuller and Lucas 2014). Race *guinea* they saw as emerging in West Africa from primitive *bicolors* selected for tolerance of high rainfall, after which *guinea* spread back eastwards. Snowden (1955) speculated that wild race *arundinaceum* (*Sorghum arundinaceum* (Desv.) Stapf.), found in the coastal regions of Guinea and Congo, hybridized with race *bicolor* to give rise to the local West African Sorghums (now classed as *guinea*). The origin of *caudatum* they saw as overlapping in range with that of *bicolor*, broadly in the Sudan region. They associated the dispersal of *caudatum* with “Chari-Nile” languages (an internal grouping of Nilo-Saharan languages including East Sudanic, Central Sudanic), found today in South Sudan, parts of Ethiopia, Eritrea, Darfur and Nubia. The distribution of *durra*, being historically the dominant sorghum within both India and the Near East, as well as the north-eastern coastal regions of Africa and southern Sahara, suggested to Harlan and Stemler that the *durra* race originated outside Africa, within India or the Near East, from primitive *bicolors* that had been transported east in prehistory, adapting to drier regions, dispersing later back to eastern Africa. The final race *kafir* is largely grown by Bantu speaking peoples south of the equator. As such the race was identified as having arisen within southern Africa, potentially through hybridization with local, geographically separate wild race *verticilliflorum* sorghums (Shechter and de Wet 1975).

Chronologically, while *bicolor* was identified as the earliest race, appearing before 1000 BC they then hypothesised that *guinea* was most likely the second race to emerge due to its wide distribution. The third, *durra*, was seen as having emerged in India by

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<sup>1</sup> It is worth noting that there remain some nomenclature differences between published taxonomy and that listed as accepted on [www.theplantlist.org](http://www.theplantlist.org) (accessed 28 Feb. 2016).

**Table 1.** The morphological races of sorghum (after Harlan and de Wet 1972)

	Race	Abbrev.	Characteristics
(1)	bicolor	(B)	Seed is elongated, long “clasping” glumes and “open” panicle/inflorescence
(2)	guinea	(G)	Grains round or broadly ovate, flattened on both dorsal and ventral sides and twisted between long “clasping” glumes. Panicles are large and open or loose. Often in wetter habitats
(3)	caudatum	(C)	Grains plano-convex flatted on the lower side “turtle-backed” and flat on the other. Glumes often shorter in length than grain.
(4)	kafir	(K)	Seed broadest above the middle – Panicles often compact. Spikelets sessile, ovate with “clasping” glumes like in guinea.
(5)	durra	(D)	Inflorescence compact. Spikelets sessile and often flattened, Seed broadest above the middle, but near spherical. Glumes wide, creased and differently colour to base. In drier habitats.

**Table 2.** A comparison of current binomial classification at left (followed here) and the single species taxonomy following Wiersema and Dahlberg (2007)

Selected binomial nomenclature (followed here for archaeobotanical finds)	Single species classification
<i>Sorghum verticilliflorum</i> (Steud.) Stapf. Wild progenitor complex, mostly annual, 4 races (verticilliflorum, arundinaceum, aethiopicum, virgatum)	<i>Sorghum bicolor</i> subsp. <i>verticilliflorum</i> (syn. <i>S. bicolor</i> subsp. <i>arundinaceum</i> in de Wet (1978)) Wild progenitor complex, 4 races (as left column)
<i>Sorghum drummondii</i> (Steud.) Millsp. & Chase The weed complex	<i>Sorghum bicolor</i> subsp. <i>drummondii</i> Weed complex, feral sorghum or backcrosses between subsp. <i>bicolor</i> and subsp. <i>verticilliflorum</i>
<i>Sorghum bicolor</i> (L.) Moench. Domesticate. Diploid. Includes 5 races (cf. Table 1)	<i>Sorghum bicolor</i> subsp. <i>bicolor</i> The domesticated crop, includes 5 races.
<i>Sorghum propinquum</i> (Kunth) Hitchc. Perennial wild sorghum found in South and Southeast Asia. Diploid. Hybridizes with <i>S. bicolor</i>	<i>Sorghum propinquum</i> (Kunth) Hitchc
<i>Sorghum halepense</i> (L.) Pers. Perennial wild sorghum with creeping rhizome on damp soils in Southwest Asia through the Indus (tetraploid). Hybridizes with <i>S. bicolor</i>	<i>Sorghum halepense</i> (L.) Pers

the first millennium BC, and then spreading back to Africa. Guinea they speculated was around 2000 years ago taken directly from Ethiopia to north-west India, utilizing well established existing trade networks. That kafir was absent from India led them to postulate that this race emerged in southern Africa less than 2000 years ago, after guinea had spread from Africa to India. The most recent of the races, was suggested to

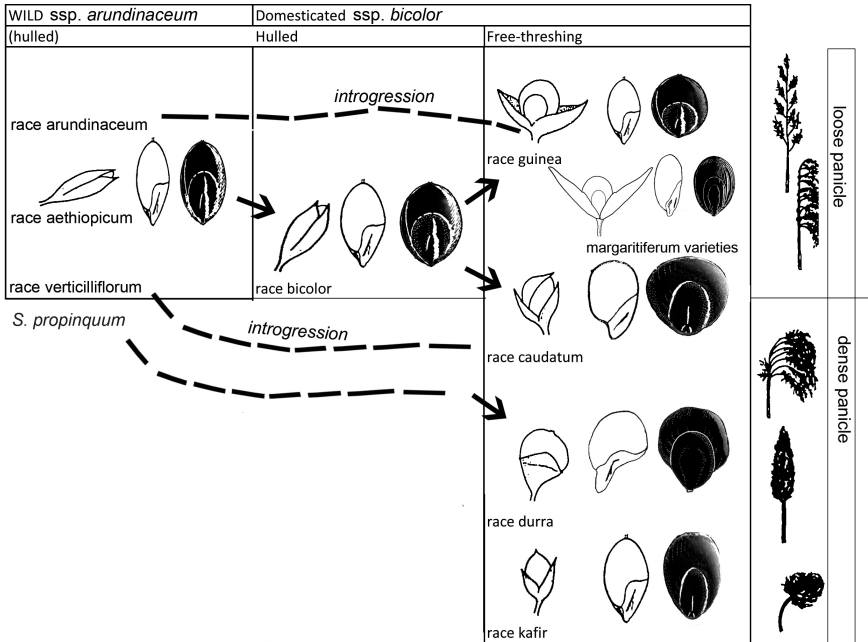
be caudatum, due to its very limited distribution. At some time, probably by the early first millennium AD, they proposed that the Indian derived durra race came back west into northeast Africa via Egypt and the Sinai, a movement that led the writers of ancient Greece and Rome to speculate that sorghum came from India. The spread of race bicolor from India into China was seen to be via Burma (modern Myanmar) spreading into Indonesia and northwards into China by at least the mid first millennium AD (Hagerty 1941; Harlan and Stemler 1976). This last saw the emergence of the Chinese kaoliang, a variety of race bicolor (Snowden's *Sorghum nervosum* Bess ex. Schult.). However, there was little archaeological evidence in the 1970s with which to corroborate this framework.

## The Races of Sorghum as seen from Genetics

While Snowden (1936) originally envisaged multiple domestications, Harlan and colleagues proposed a single origin for bicolor with later separation of guinea, durra, kafir and caudatum, each involving some degree of introgressions with local wild populations. A schema for understanding sorghum evolution in these terms is illustrated in Fig. 1. In recent years a large number of genetic studies have examined the division of the five main races. In the majority of studies some clear differentiation has been seen between the later races; guinea, durra, kafir and caudatum, with race bicolor showing much less clear differentiation (Deu et al. 1994, 2006; Casa et al. 2008; Mace et al. 2008; Brown et al. 2011). An earlier study demonstrated that cultivars were most closely aligned with wild populations of sorghum within central-northeast Africa (Aldrich and Doebley 1992). This study and others also note two to three strongly differentiated haplotype groups highlighting the problems of differentiating between potentially separate domestication events and later migration events with introgression from local wild populations (de Alencar Figueiredo et al. 2008; cf. Lin et al. 2012).

Genetic studies, while recognizing the separation of the races, also note divisions within them. Guinea showed separation into four clusters; two closely related in West Africa, and two related clusters in Southern Africa and Asia (Deu et al. 1994, 2006). Further the populations of sub-race margaritifera of West Africa, with small spherical grains, clearly separated from other guineas (Deu et al. 1994, 2006; Casa et al. 2008; de Alencar Figueiredo et al. 2008; Brown et al. 2011; Ramu et al. 2013; Luo et al. 2016), showing close affinity to local wild and weedy sorghums (Billot et al. 2013; Morris et al. 2013) of wild race arundinaceum. Other studies also demonstrate a genetic affinity between guinea populations of southern and Eastern Africa with those of South Asia (Folkertsma et al. 2005), supporting a hypothesis suggesting the migration of this crop during Indian Ocean maritime trade networks from the 8<sup>th</sup> century AD onwards (see Boivin et al. 2014). Other studies show Indian guineas clustering more closely with durras (Morris et al. 2013), which might be accounted for by ongoing introgression across Indian crop populations, or both having introgression from wild *Sorghum propinquum*.

These studies demonstrate the need to reclassify some of the sub-races. One clear example is the West African kaura group (Snowden's *S. caudatum* var. *kerstingianum*) which clusters with guineas, not with durra-caudatums into which they are traditionally



**Fig. 1.** The sorghum evolutionary framework relating wild, domesticated and the major domesticated races. Horizontal axis show seed dispersal from wild shattering to free-threshing; vertical axis the development of panicle form/density. Solid arrows indicate the main direction of evolution and improvement. Dashed lines indicate hypothetical introgression from wild populations.

ascribed (Brown et al. 2011). Genetically kaura sorghum is then derived from race guinea, but later evolved tighter, compacted panicles and shorter glumes, characteristic of the durra and caudatum races respectively, perhaps in response to the drier regions of northeast Nigeria, where they are most often found.

While the general implication is that genetic studies broadly support the morphological separation of the races, one of the largest and most recent studies by Billot et al. (2013) highlights the importance of geographic distribution with respect to genetic differentiation. For example, eastern Asian caudatums, durras and bicolors appear more closely related to each other than to these same races in Africa (Billot et al. 2013). What remains unclear is whether this implies that free-threshing forms evolved many times in parallel or whether the movement of free-threshing races was followed by extensive introgression with locally adapted landraces of bicolor. The latter is perhaps more parsimonious, requiring fewer selection events for free-threshing morphotypes. What is needed is an understanding of the particular alleles that create the various free-threshing morphotypes.

Durra showed strong separation in most studies (Deu et al. 2006; Perumal et al. 2007; Casa et al. 2008; Mace et al. 2008; Brown et al. 2011). Within the study conducted by Brown et al. (2011) Asian durra sorghums clustered together, but were

most closely related to durras from Somalia, and Ethiopia. Other studies demonstrate similarities between northern Chinese Kaoliangs (traditionally classified as bicolor due to their persistent husks; Snowden's *S. nervosum*) with durra types, especially from Yemen (Morris et al. 2013). This might suggest that durra evolved from the same South Asian populations that dispersed to China, a process still poorly documented archaeologically, but probably dated to the early to mid-first millennium AD from northeast India via Yunnan (Hagerty 1941; Bonjean 2010).

Those assigned to the unfortunately named kafir (Snowden's *S. cafrorum*) exhibited strong separation in all studies (Deu et al. 1994, 2006; Casa et al. 2008; Mace et al. 2008; Brown et al. 2011). The low diversity seen within kafir, along with West African guineas, suggests bottlenecks relating to geographical isolation (Casa et al. 2008; see Deu et al. 2006). A study on photoperiod indicated that guinea types brought from West Africa into southern Africa, potentially gave rise to kafirs, adapted to longer-day ecosystems. Perhaps associated with Bantu-speaking groups that crossed the central African rainforest and migrated slowly southwards (cf. Klein et al. 2015). This would represent the west and southwest Bantu stream via the Sangha River Interval (sensu Grollemund et al. 2015), implying an arrival in southern Africa later than the initial sorghum associated with early Iron Age Eastern Bantu migrants.

Caudatums split into two clusters, the main one geographically centred on the Great Lakes Region of East Africa e.g. Tanzania, Malawi, Zambia, Kenya, Uganda (Deu et al. 1994, 2006), but stretching into Ethiopia and Sudan (Brown et al. 2011). However, many studies demonstrated sorghum lines assigned to caudatum outside this geographical area falling into separate groups (see Deu et al. 1994, 2006; Mace et al. 2008; Billot et al. 2013). Studies also separated out zerazera-caudatums (Snowden assigned as a form of *S. caudatum* var. *durum*), found mainly in the border region between Sudan and South Sudan but stretching southeast, from West African and Central Sudanese guinea-caudatums (probably genetically guineas) and other caudatums centred mainly on South Sudan, Uganda and northeast Congo, with some further groups in South Africa (Sukumaran et al. 2012; Casa et al. 2008).

Many studies imply at least two separate introductions of sorghum into Asia (Deu et al. 2006). The first was an early bicolor that evolved into durra and Chinese kaoliang (*S. nervosum*). The second presumably was an east African guinea variety traded from the Swahili world. The origins of these bicolors in northern Sudan would explain the genetic affinities to some central African caudatums (cf. Billot et al. 2013), which also evolved in northern Sudan. Guinea sorghums often have a hard, corneous endosperm, making the grains suited to whole-grain boiling, and these forms are popular in the tribal zones of eastern and central India (Appa Rao et al. 1996). Whether or not caudatum sorghums in India represent a third ancient introduction, a recent introduction, or rather are just morphologically similar adaptations from durra and guinea/kafir types remains to be determined. Notably, one caudatum type from India examined by Brown et al. (2011) was genetically closer to kafir, implying that the transition between guinea/kafir and caudatum morphology (i.e. a c. 45° twist in the grain primordium) represents a simple genetic shift that occurred locally in Indian guinea sorghum.

While most genetic research is congruent with the conventional view of a single major domestication episode of sorghum, followed by differentiation into races during and after geographical dispersal, a high profile study of non-shattering genetics argued

for three independent domestications, two in northern Africa and one in the southeast (Olsen 2012). This is based on the identification of three alternative dominant mutations to the sorghum gene *Sh1* on chromosome 1 that turn off the abscission zone at the base of the spikelet, and have differing geographical distributions. One of these mutations (Tx623) is found in kafir, bicolor and guinea sorghum races from southern Africa, another (Tx430) is largely restricted to caudatums throughout Africa, and a third (SC265) is found across all races except kafir, in both Asia and Africa (Lin et al. 2012: Table S1). Before considering the implications of this study, some caution is warranted, as early claims to have identified the key mutation for non-shattering in rice domestication (e.g. Li et al. 2006, 2007) have been overturned with evidence that the interaction of several loci is involved and that these evolved sequentially, some probably only in limited post-domestication lineages (e.g. *Oryza qsh1*) (Ishii et al. 2013; Htun et al. 2014). If multiple initial domestication episodes of race bicolor had involved other loci that also caused reduced shattering, then a higher degree of non-shattering might be expected to be seen as advanced free-threshing races evolved, much as the free-threshing *Q* gene was added to the non-shattering *Br1* mutations that was involved in hulled wheat domestication (Li and Gill 2006; Fuller and Allaby 2009: 251). Thus we predict that sorghum *Sh1* was involved in post-domestication improvements to non-shattering rather than to the initial evolution of non-shattering during race bicolor domestication. This may be further supported by the many race bicolor accessions reported as having only “moderate” non-shattering phenotypes in the USDA database (NPGS 2016), whereas only strongly shattering domesticated and non-shattering wild accessions were included in the study of Lin et al. (2012). Looking more closely at these data (Lin et al. 2012: Table S1), they can be reduced to just two pathways as the kafir type (Tx623) variant could be derived from further mutations (mainly a large deletion and 2 SNPs) to the caudatum type (Tx430) haplotype. By contrast the third variant (SC265) appears to be caused by a small number of different SNPs, shared across a range of races and regions, including widespread race bicolor accessions. This could be congruent with evolution of *Sh1* twice, once within the western, the other towards the eastern parts of the zone of initial north Sudanese sorghum domestication (see archaeobotanical discussion, below). These mutations were plausibly additive to other alleles, not yet characterized, that are associated with earlier moderate non-shattering phenotypes (of which there are many varieties among Sudanese race bicolor, but none of them were included in the genetic study of Lin et al. 2012).

## **An Updated Archaeobotanical Framework of Sorghum Domestication**

Domestication represents a number of adaptations on the part of a plant to being cultivated and harvested by people (see Harlan et al. 1973; Fuller et al. 2010, 2014). Key changes include loss of natural seed dispersal (visible archaeologically in spikelet bases), changes in germination traits (not easily visible archaeologically), and increase in grain size, most notably grain width (measurable archaeologically). To date,

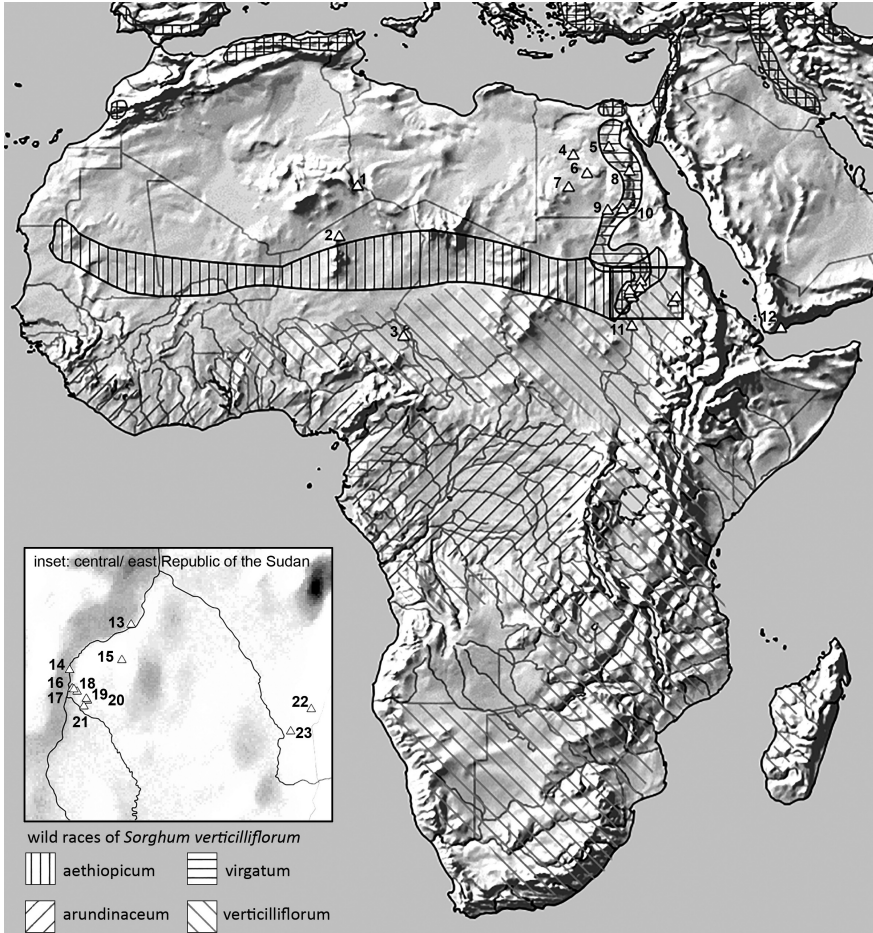


however, few archaeobotanical assemblages have allowed these domestication traits to be documented for sorghum.

To begin wild sorghum was likely gathered with baskets as stands of wild-type shattering plants matured. Such spikelets would still have had tight fitting husks and hence required dehusking, then winnowing, to obtain clean grain. With the evolution of non-shattering (domesticated) type plants, threshing and a further winnowing stage would be required, in order to break the rachises and secondary branches and hence separate the spikelets from the harvested panicles. Possibly winnowing/sieving practices already existed following the basket gathering of wild spikelets, in order to remove lighter plant parts and seeds from other wild species collected at the same time; the spatial patterning in wild sorghum versus other grasses in Nabta Playa contexts could be indicative of such practices (cf. Wasylikowa and Dahlberg 1999, 2001).

The development of non-shattering (domesticated) plants would have necessitated more labour input for processing, while new techniques and technologies of harvesting, such as sickles, would have been promoted. Following the trends for other cereals, cultivation would likely have selected for larger grains, leading to increased yields (Fuller et al. 2010). Subsequent evolution of the free-threshing sorghum races would have reduced and shifted the labour investment in processing. Grains would no longer have needed to be routinely husked and winnowed, but the removal of chaff during threshing would potentially have prolonged winnowing operations following the harvest. As such practices were likely conducted seasonally and in the field, free-threshing sorghum may be less prone to preservation by charring than race *bicolor*. The dense panicles in some advanced races also facilitated harvesting, as well as increasing yields. Thus when considered in terms of harvesting, processing and related aspects of morphology, we can outline the morphological variation of sorghum, represented by its domestication and racial evolution (Fig. 1).

The first step in studying domestication is reconstructing the distribution of wild progenitor populations for the period in the past when cultivation is likely to have begun (Fig. 2). However, the distribution of these populations today is quite different from what they would have been at the start of the Holocene. Under the wetter conditions of the early to middle Holocene, the era of a Green Sahara (Kröpelin et al. 2008; Manning and Timpson 2014), the savannahs with sorghum were located much further north, approximately midway across the modern Sahara. This is supported by archaeobotanical finds of morphologically wild sorghum in the Western Desert of Egypt and southwest Libya (Fig. 2), dating to the early to middle Holocene, the earliest at Nabta Playa E-75-6, c. 8000 BC (Wasylikowa and Dahlberg 1999), with later finds from Farafrā, c. 5800 BC, and Abu Ballas, c. 3750 BC (Barakat and Fahmy 1999). These sites provide no evidence for cultivation but it is likely that wild grains were collected (see Wasylikowa and Dahlberg 2001). Continued wild sorghum use in the 5<sup>th</sup> and 4<sup>th</sup> millennium BC, is indicated by impressions in pottery from central Sudan (Magid 1989, 2003; Stemler 1990) in the Khartoum region. These comprise Neolithic societies with evidence for domesticated sheep, goat and cattle (Gautier and van Neer 2006; Chaix and Honegger 2015). This shift in the evidence is congruous with a southerly retreat of wild sorghum stands as the Sahara dried and expanded. Possibly this involved southward migrations, and would fit with Nilo-Saharan proto-language reconstructions (Ehret 2014) and evidence for the southward spread of pastoralism. The



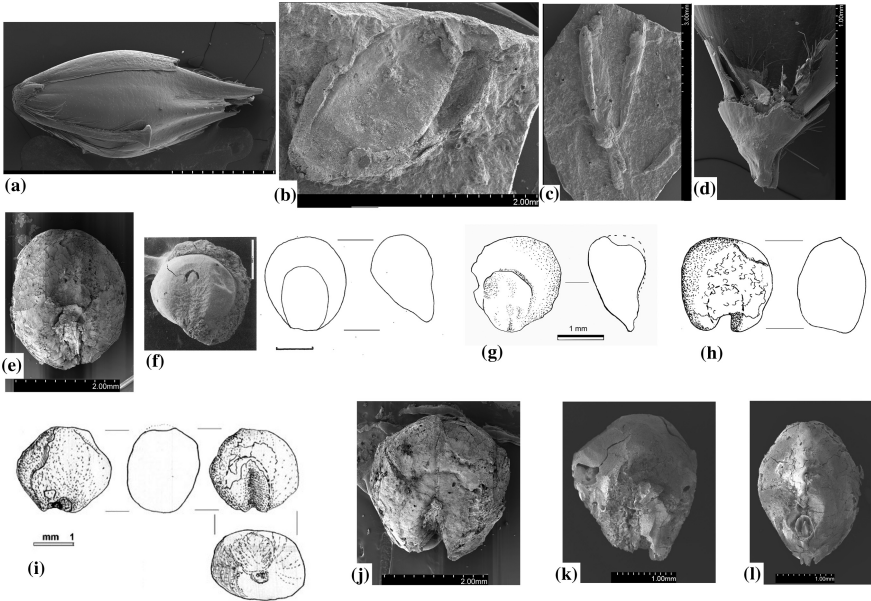
**Fig. 2.** Distribution of wild modern and archaeological sorghum. Hatched area represents approximate/potential modern distributions of wild sorghum races (*S. verticilliflorum*) after Harlan and Stemler (1976). Triangles indicate archaeological sites with finds of morphologically wild sorghum: 1. Takarkori (7000–6200 BC), 2. Adrar Bous (3500–1500 BC), 3. Kursakata (1000–200 BC), 4. Farafra Oasis (6060–5560 BC), 5. Amarna (1365–1345 BC), 6. Dalkleh Oasis sites (8300–7000 BC), 7. Abu Ballas (4500–3000 BC), 8. Tutankhamun’s tomb (1328 BC), 9. Nabta Playa E-75-6 (8100–7900 BC), 10. Qasr Ibrim (1000–300 BC), 11. Rabak (4500–4300 BC), 12. Sabir (1000–800 BC), 13. El Kadada (4000–3000 BC), 14. Shaheinab (4100–3300 BC), 15. Shaqadud (3500–2200 BC), 16. El Zakiab (4300–4000 BC), 17. Kadero (3800–3600 BC), 18. Um Direiwa (5000–3800 BC), 19. El Mahalab (6650–5800 BC), 20. Sheikh el-Amin (7000–6450 BC), 21. Sheikh Mustafa (4400–3300 BC), 22. Mahal Teglinos K1 (2000–1700 BC), 23. Khashm el Girba KG23 (3500–3000 BC).

evidence presumably relates to exploitation of *S. verticilliflorum* race aethiopicum, while other wild sorghums so far lack evidence for exploitation. Wild *Sorghum* sp. identified in first millennium BC Yemen (de Moulins et al. 2003) seems most likely race verticilliflorum on geographical grounds.

While Stemler (1990) identified a single impression of a possible “domesticated-type” spikelet with a torn rachilla from Um Direiwa (> 3800 BC) this might still relate to the harvesting of green or near-ripe wild sorghum. However, a larger dataset of sorghum pottery impressions has recently come to light dating to the mid to late fourth millennium BC at Khashm el Girba KG23 near Kassala (Winchell et al. 2017). These new data consist of 265 plant impressions of sorghum grains and spikelets preserved in sherds of Khordhag plain pottery of the Butana group period from site KG23 (see Winchell 2013 for archaeological details). Among these are 16 impressions from 9 sherds, that clearly preserve evidence for non-shattering sorghum spikelet bases with torn rachilla (Fig. 3a, b), while 18 other impressions spread across 13 sherds preserve wild type smooth spikelet bases (Fig. 3c, d). A further 17 impressions were identified as recognizably immature. Taken together these data suggest the harvesting of cultivated populations undergoing domestication.

These sorghum spikelets, comprising mature non-shattering types, mature shattering wild types, and immature “green” types, are consistent with the harvesting of populations still displaying asynchronous ripening. Hence, during these early stages of pre-domestication cultivation, harvesting was conducted before all plants had matured to avoid grain loss caused by the still high presence of wild-type shattering plants. This same practice has been observed during the earlier stages of pre-domestication cultivation for rice in the Lower Yangtze, where the “green” harvesting of rice resulted in charred archaeobotanical assemblages that included immature spikelet bases, wild type spikelet bases and non-shattering domesticated types (Fuller et al. 2010). These finds, together with those from the early second millennium BC at Kassala K1 (Beldados and Costantini 2011; Beldados et al. 2018) suggest a protracted period of pre-domestication sorghum cultivation from before 3500 BC to perhaps c. 1700 BC. These data are consistent with the protracted domestication episodes of 2000–4000 years documented for other cereals, including wheats, barley and rice (Fuller et al. 2014).

These new finds indicate that morphologically domesticated sorghum was present in eastern Sudanese populations, even if these types were not fully dominant before 3000 BC. They fit with the region of domestication hypothesized by Clark (1984), lying within the confluence of the Blue and White Nile, and the Atbara River, but are earlier than he anticipated. Of particular importance the Kassala evidence pre-dates finds in India, where domesticated sorghums are well established as being present by at least the early second millennium BC (Fuller 2003a; Fuller and Boivin 2009). Although grains from the Harappan site of Kunal are considered earlier (c. 2400 BC) (Saraswat and Pokharia 2003), these are not-directly dated and full details of their context are not available, so caution is warranted in accepting them as mid third millennium BC. It should be noted also that older reports of sorghum from the Arabian Peninsula are problematic. Impressions from the site of al-Raqlah in Yemen, 3000–2500 BC (Costantini 1990) are poorly illustrated and hard to accept as legitimate (Rowley-Conwy et al. 1997; Fuller 2002, 281–2; de Moulins et al. 2003; Fuller and Boivin 2009): these are too round for an early bicolor form that would be expected at



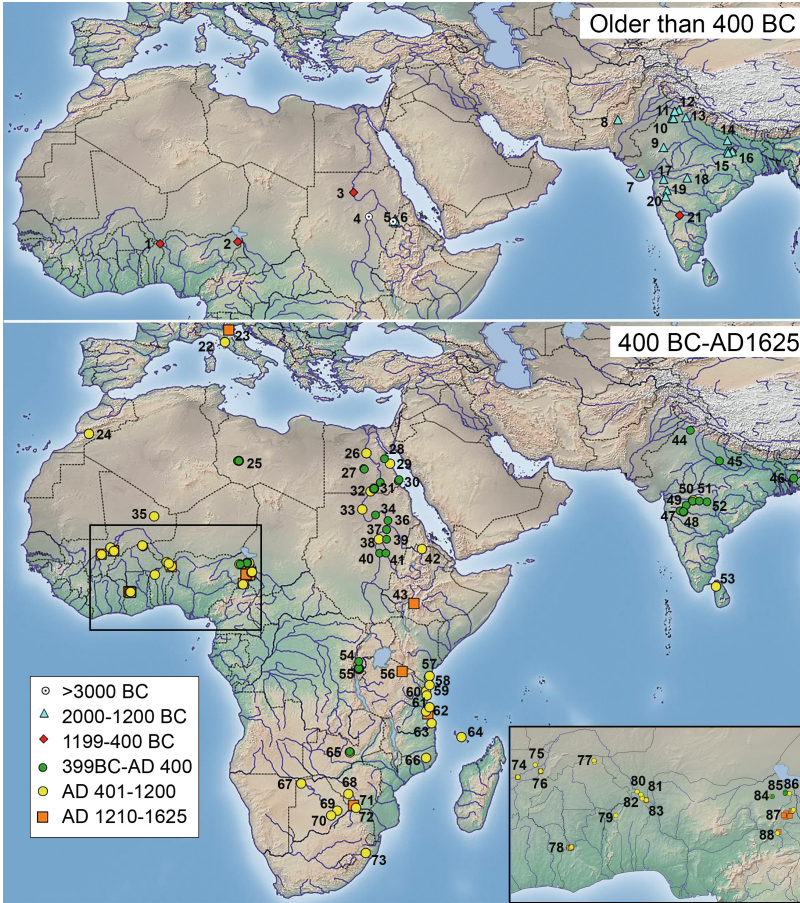
**Fig. 3.** Examples of archaeological sorghum relating to early domestication and racial differentiation: A. modern wild shattering spikelet of *S. verticilliflorum*; B. wild-type sorghum spikelet impression in ceramics, Khashm el Girba KG23 (studied by the authors; Winchell et al. 2017); C. domesticated, sorghum spikelet base impression with rachilla, Khashm el Girba KG23 (studied by the authors; Winchell et al. 2017); D. modern domesticated spikelet base, race bicolor, after grain removal; E. race bicolor type grain, Early Historic Paithan, Maharashtra, India (Fuller in press); F. race caudatum type grain, SEM/sketch of dorsal and lateral, Tinda B, Libya (after Pelling 2005); G. caudatum(?) type grain, Kawa, Nubia, dorsal and lateral view (after Fuller 2004); H. caudatum type grain, poorly preserved surface in dorsal and lateral views, Early Iron Age Kabusanze, Rwanda (after Giblin and Fuller 2011); I. caudatum type grain, Middle Iron Age Panga Ya Saidi, Kenya (after Shipton et al. 2013); J. durra type grain, Early Historic Paithan, Maharashtra, India (Fuller in press); K. durra type grain, Meroitic Hamadab, Sudan (authors, unpublished); L. bicolor type grain, Meroitic Hamadab, Sudan.

such an age. Clearly mis-identified are also the often cited impressions of sorghum from third millennium BC Hili in Oman (Cleuziou and Costantini (1980), Fig. 2; first questioned by Willcox (1992)), which show fruits attached on the jointed ends of flared pedicels, that are consistent with *Asphodelus* sp. (Liliaceae), a common weed of Arabian wheat and barley cultivation in macroremains assemblages of the period (Tengberg 2003). Taken together these data suggest that cultivated, at least partially domesticated, if not near fully domesticated sorghum was rapidly transferred from eastern Sudan/Eritrea to western India (Gujarat) by the start of the second millennium BC. It is not clear whether there was a geographically intermediate stage of sorghum cultivation in Yemen or southern Oman (Dhofar) (for further discussions of the mechanisms and cultural context, see Boivin and Fuller 2009). Once separated from

wild gene flow and adopted into the established wheat, barley or millet cultivation regimes it is probable that the non-shattering traits became fixed in populations relatively quickly, thereby reaching full domestication more or less upon its arrival in Western India. Therefore contrary to the Haaland (1995) hypothesis there is no reason to postulate the transfer of a morphologically wild sorghum to India and a return voyage of domesticated race bicolor. Nevertheless, further systematic study of early Indian sorghum is needed to trace domestication traits and racial evolution within South Asia, although most early finds are plausibly race bicolor (e.g. Figure 3e).

Indian historical linguistics are unable to shed further light on this issue. Indic terms for sorghum (e.g. Prakrit *gajja*, Sanskrit *yavanala*) are likely derived from older roots for barley. Those in Dravidian languages possibly represent a semantic shift from an older millet term, e.g. for *Brachiaria ramosa* (Southworth 2006), as sorghum appears to reconstruct to an earlier stage of the Dravidian languages than either pearl millet or wheat (Fuller 2003b).

Several hypotheses derived from historical linguistic inferences suggest the migration of sorghum-growing farmers into various parts of Africa, although discrepancies with available archaeobotanical data remain, especially in terms of the inferred date of these dispersals. For example, while early Nilo-Saharan speakers focused on pastoralism in the eastern Sahara and Sahel, probably alongside wild sorghum harvesting, new terms for cultivation appear later in the Proto-Saharo-Sahelian stage (Ehret 2014), potentially attributed to the later middle Holocene, e.g. c. 4000 BC. As reviewed above archaeobotanical finds from the central and eastern Sudan suggest cultivation was established by 3500 BC with morphological domesticated types already present. As such sorghum cultivators a millennium or more earlier might be sought further north. However, it is hard to determine whether sorghum cultivation in this region, which generally shows local continuity through much of the earlier to middle Holocene (Winchell 2013), was brought by immigrants arriving from the north, although cattle, sheep and goat must have spread this way. Ehret (2011) also inferred that Afroasiatic speakers, from the Cushitic lineage probably had sorghum cultivation when they moved south from the Southern Atbai region into the Ethiopian highlands (by c. 3500 BC). However, it is hard at present to reconcile this with the, albeit limited, archaeobotanical data that initially show just wheat and barley in the 1<sup>st</sup> millennium BC, and only later finds of sorghum and the indigenous Ethiopian tef (D'Andrea and Wadge 2011). Nevertheless the new evidence for sorghum cultivation in the 4<sup>th</sup> millennium BC, and presumably through the early second millennium BC, in eastern Sudan might support this. Further, the arrival of domesticated sorghum in India by c. 1700 BC (Fuller 2003a; Fuller and Boivin 2009), makes it highly plausible that during the third millennium BC sorghum-growing agropastoralists were expanding through the Eritrean region and hence potentially further south into parts of Ethiopia.



**Fig. 4.** Map of the distribution of archaeological domesticated sorghum in broad time slices, 1. Alibori SIII, 2. Mege, 3. Kawa, 4. Um Dereiwa, 5. Khashm el Girba, 6. Kasala K1, 7. Rojdi, 8. Pirak, 9. Ojiyana, 10. Banawali & Kunal, 11. Rohira, 12. Sanghol, 13. Hulas, 14. Imlidh-Khurd, 15. Malhar and Raja-Nala-Ka-Tila, 16. Senuwar, 17. Kaothe (intrusive?), 18. Tuljapur Garhi, 19. Daimabad, 20. Inangaon, 21. Piklihal, 22. Miranduolo, 23. Ferrara, 24. Ingiliz, 25. Jarma & Tinda, 26. Kom el-Nana, 27. Karga Oasis, 28. Mon Claudianus, 29. Qesir al-Qadim, 30. Berenike & Shenshef, 31. Wadi Qitna, 32. Qasr Ibrim, 33. Faras East, 34. Umm Muri, 35. Essouk, 36. Dangeil, 37. Hamdab & Meroe, 38. Soda, 39. Jebel Qeili, 40. Jebel Tomat, 41. Abu Geili, 42. Axum, 43. Tuwatey Zonga Cave, 44. Sanghol, 45. Sanchankot/Ramkot, 46. Wari-Bateshwar, 47. Nevasa, 48. Paithan, 49. Bhokardan, 50. Bhon & Paturda, 51. Bhatkuli, 52. Paunar, 53. Mantai, 54. Kabusanze, 55. Kabuye (possible pollen), 56. Engaruka, 57. Mgombani, 58. Panga Ya Saidi, 59. Tumbe, 60. Fukuchani, 61. Unguka Ukuu, 62. Juani Primary School & Kilwa & Songo Mnara, 63. Mikindani sites, 64. Old Sima, 65. M'teteshi & Mondake, 66. Yakota, 67. Nqoma, 68. Leopard's Kopje, 69. Kgaswe, 70. Matlhapaneng, 71. Mapela, 72. Schroda, 73. Magogo, 74. Dia-Mara & Sorotomo, 75. Dia-Shoma, 76. Jenne-jeno, 77. Oursi hu-beero & Kolel Nord, 78. Banda 13 & 27 & 41 & Kuulo Kataa & Ngre Kataa, 79. Yohongu, 80. Pekinga, 81. Tintin, 82. Birnin Lafiya & Kantoro, 83. Madekali, 84. Elkido North & Dorota, 85. Mege & Kursakata, 86. Daima, 87. Kayam & Jidderi Saoudjo & Balda Tagamre & Tthere & Goray & Salak & Mowo & Louggero, 88. Douloumi & Be. Key sources in addition to those cited in the text, include: (Fuller 2014; Mitchell 2002; Logan 2012; Nixon et al. 2011; Ruas et al. 2011; Delneuf 1995).

## Dispersal and Diversification of Sorghum: The Archaeobotany of the Races

After its establishment as a crop in parts of Sudan, e.g. Bayuda to Southern Atbai belt, morphologically domesticated sorghum dispersed and eventually diversified. Archaeobotanical finds, although still few and far between in Africa allow us to sketch the arrival time of sorghum into various regions and thereby infer how quickly it spread (Fig. 4). In some cases sorghum is likely to have diffused as part of a package of crops and animals with migrating farmers, although sorghum was also transferred across language families.

The westward dispersal of sorghum has not been tied to linguistically inferred ethnic migrations, but evidence for sorghum in northern Benin prior to the local Iron Age (c. 700 BC, see Champion and Fuller, 2018), and probable evidence for sorghum at Mege, near Lake Chad, at 800–400 BC (Bigga and Kahlheber 2011), indicate a westward diffusion in the first millennium BC. Evidence for pearl millet as early as sorghum in India, i.e. 1900–1700 BC, and possible cowpea (Fuller 2003a; Fuller and Boivin 2009) indicate that established cultural networks allowed pearl millet to diffuse eastward from West Africa probably shortly after the mid third millennium BC. Pearl millet is a crop highly suited to mobile agro-pastoralists with a short growing season and low water requirements, which may have facilitated its rapid spread eastwards over less than a millennium along the southern margins of the Sahara (Manning and Fuller 2014). These same social networks are likely to have been responsible for the less rapid spread of caudatum westwards, after free-threshing caudatum evolved in the central Sudan.

Two distinct westward trajectories can be advocated. Race bicolor likely dispersed westwards across the southern savannah, towards Nigeria, Cameroon and Benin, early in the first millennium BC, and some grains from Birnin Lafiya in Benin suggest local evolution of guinea types by the early centuries AD (Table 3), likely involving gene flow from wild race arundinaceum sorghums. By contrast more northerly and Sahelian dispersal for caudatum can be postulated, presumably from origins in Sudan. This is indicated by finds at Jarma in the Fezzan in Libya by 100 BC (Fig. 3e; Pelling 2005, 2007), Jenne-Jeno, Mali by the 6<sup>th</sup>/7<sup>th</sup> century AD, and Daima near Lake Chad in the 9<sup>th</sup> or 10<sup>th</sup> century (Connah 1967, see Table 3). The still un-replicated evidence from Kawa in Nubia, 800–400 BC, might yet hint at earlier origins for race caudatum (Fig. 3f). Meanwhile the caudatum like grains from Kaothe in India probably should be regarded as intrusive, as suggested by Kajale (1990).

Moving to the south of the Ethiopian highlands evidence for sorghum is much later. Securely identified and dated finds come only from the early centuries AD in East Africa, including third or fourth century AD finds from Kusbunze (Fig. 3g) (Giblin and Fuller 2011), and from Zimbabwe, Leopard's Kopje, in the 10<sup>th</sup> or 11<sup>th</sup> Century AD (Huffman 1974; Mitchell 2002, 274). De Wet (1977) suggested the latter, based on geography rather than morphology, could represent an early southern African guinea. Along the East African coast and near shore islands, sorghum is present in

**Table 3.** Reports of archaeological sorghum referred to various free-threshing races

Site	Country	Age	Sorghum Race	Sources/Comments
Jarma (Old Germa)	Libya	400 BC–AD 100	Caudatum	Pelling (2005, 2007)
Daima	Nigeria	AD 800–1000	Caudatum	(Harlan and Stemler 1976; de Wet 1977)
Kabusanze	Rawanda	AD 275–400	Caudatum	Giblin and Fuller (2011)
Panga Ya Saidi	Kenya	AD 750–950	Caudatum	Id. DQ Fuller, in Helm et al. (2012), Shipton et al. (2013); see Fig. 5
Mogambani	Kenya	AD 765–980	Caudatum	Identified by DQ Fuller, in Helm et al. (2012), Shipton et al. (2013)
Old Sima	Comores Islands, Madagascar	c. 900 AD	Caudatum	the authors (see Crowther et al. 2016)
Kaothe	India	1900–1500 BC (?)/intrusive (?)	Caudatum (?)	Kajale (1990); comments in Fuller (2003b)
Jenne-Jeno	Mali	c. AD 600	Caudatum (and Bicolor)	Identified by Harlan, in McIntosh (1982)
Kawa	Sudan	800–400 BC	Durra (?)/Caudatum (?)	Fuller (2004); high C13 raises questions about identification
Paithan	India	AD 0–400	Durra (and Bicolor)	Fuller in press
Meroe	Sudan	100 BC–AD 300	Durra (and Bicolor)	ID by Harlan, in Shinnie and Anderson (2004)
Hamadab	Sudan	50 BC–AD 350	Durra (and Bicolor)	Identified by DQ Fuller, unpublished data
Qasr Ibrim	Sudan	From AD 550	Durra (and Bicolor)	(Harlan and Stemler 1976; Rowley-Conwy 1991; Clapham and Rowley-Conwy 2007)
Soba	Sudan	From AD 600	Durra	Van der Veen and Lawrence (1991)
Quesir (Myos Hormos)	Egypt	From AD 1000	Durra (and Bicolor)	Van der Veen (2011)
Birni Lafiya	Benin	AD 200–800	Guinea (and Bicolor)	(see Champion and Fuller, 2018)

Middle Iron Age levels from the second half of the first millennium AD, e.g. at Panga Ya Saidi in southeast Kenya, Pemba, Zanzibar and Mafia Islands (Walshaw 2010; Boivin et al. 2013; Crowther et al. 2014, 2016). Many of these finds include grains resembling caudatum (Fig. 3H; Table 3), fitting with the hypotheses that caudatum, evolved in the Sudan (Harlan and Stemler 1976; Brown et al. 2011), and was transferred from Nilo-Saharan speaking farmers to the early dispersing Bantu near the southern Sudanese region as Bantu farmers moved around the rainforest (Ehret 1973; Schoenbrun 1993; Boivin et al. 2013).



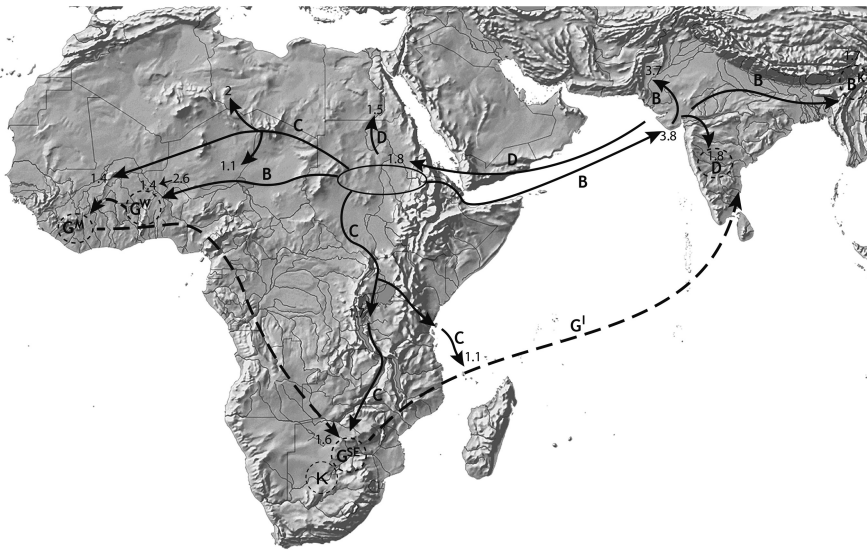
The general pattern in all of these areas of East Africa is that the earliest farming is associated with an eastern Bantu crop package, including pearl millet, cowpea, baobab, and sorghum, with finger millet appearing later (Crowther et al. 2016). Small quantities of crops derived from Asia across the Indian Ocean arrived on African islands from the 8<sup>th</sup> century AD, including rice (*Oryza sativa*), mungbean (*Vigna radiata*), cotton (*Gossypium* sp.), and coconut (*Cocos nucifera*). Therefore, we lack any firm evidence for contact between tropical Asia and eastern Africa south of Ethiopia earlier than c. AD 700, despite the distribution of taro, Asian yam, and bananas in continental Africa that have been suggested to relate to much earlier trans-Indian Ocean transfers (e.g. Blench 2009; see also Fuller and Boivin 2009; Boivin et al. 2014). The presence of apparent race guinea in parts of India, has however suggested Indian Ocean transfers out of southeast Africa, later than the posited Bronze Age circum-Arabian transfer of race bicolor (see Fuller 2003a). Genetic data indicate southeast African guineas derive from margaritifera types in the West African rainforests, which imply a dispersal from western to southern African and then across the Indian Ocean.

Archaeobotanical finds referred to as durra are restricted to regions where durra is prominent today, including peninsular India and Nubia (Sudan). Durra types are present at the early historic city of Paithan, Maharashtra (Fig. 3i) from nearly 2000 years ago, while finds from Meroe and nearby Hamdab (Fig. 3j, k) suggest a broadly similar age in Nubia (Table 3). The northerly dispersal of durra down the Nile to Lower Nubia is seen from probable intermediate durra-bicolor morphotypes at late post-Meroitic Qasr Ibrim (c. AD 500), eventually dominating in the Christian and Medieval periods (Rowley-Conwy et al. 1999; Clapham and Rowley-Conwy 2007). Nevertheless, race bicolor remained important in this region, as indicated by 12<sup>th</sup> century AD finds at Nauri near the Third cataract (Fuller and Edwards 2001), and Qesir on the Red Sea Coast (van der Veen 2011); the illustrated sorghum from Byzantine Kom el-Nana is also race bicolor (see Smith 2003). The hulled grains of race bicolor are likely more resilient under various storage conditions, and less prone to bird predation, hence still have advantages over the free-threshing races. The transfer of sorghum into Mediterranean agriculture, in central and northern Italy (e.g. Bosi et al. 2009; Buonincontri et al. 2014), notably also involved race bicolor having similar cultivation, storage and processing requirements to *Setaria italica* and *Panicum miliaceum* that were already well-established.

## Sorghum Diversification and Dispersal: A Revised Framework

We are now in an improved position to outline the history of sorghum diversification and dispersal (Fig. 5) as a revision to the schema of Harlan and Stemler (1976). While genetics has revealed a more complex series of interregional relationships than was originally envisaged in the five race classification, archaeobotanical specimens that can be referred to various advanced free-threshing races, or as plausibly free-threshing, provide a framework of dates for when races differentiated and arrived in different

regions (Table 3). We assume that bicolor spread along all of these paths, either accompanying or preceding the advanced free-threshing races (Fig. 5). The overall pattern suggests sorghum domestication and subsequent evolution of caudatum in the central/eastern Sudan region with dispersals east, west and southward. These dispersals likely led to introgression with local wild races, providing the genetic materials for various local ecological adaptations, including some of the variants in photoperiodicity genes that helped to alter and broaden the seasonality of sorghum. This overall pattern illustrates the importance of *introgressive capture* (sensu Larson and Fuller 2014) in structuring the genetic geography of domesticated sorghum to resemble pre-existing geographical patterning in wild diversity. It is this introgression that likely lies behind erroneous claims for multiple domestications (e.g. Shechter and de Wet 1975; Olsen 2012), as well the clustering of South and East Asian sorghum germplasm, regardless of race (Billot et al. 2013), probably through introgression of domesticated sorghum



**Fig. 5.** A revised framework of the dispersal and diversification history of domesticated sorghum, based on the archaeobotanical and genetic evidence reviewed in this paper. Solid oval indicates zone of domestication of early race bicolor and subsequent evolution of race caudatum; dashed ovals indicate hypothetical zones for the evolution of other races or varieties. Solid arrows indicate trajectories inferred from archaeobotanical evidence, dashed arrows indicate hypothetical dispersal inferred from genetics without archaeobotanical support. Numbers indicate approximate age in years before AD 2000 for arrival time or evolutionary event. Letters on arrows indicate races or varietal groups inferred for each dispersal trajectory: B = bicolor race, B<sup>K</sup> = Chinese Kaoliang sorghum group within race bicolor, C = caudatum race, D = durra race, G<sup>W</sup> = race guinea, west African group, G<sup>M</sup> = race guinea, margaritifera varieties (= *S. margaritifera* Stapf.), G<sup>SE</sup> = race guinea, southeast African group, G<sup>I</sup> = race guinea, Indian group, K = race kafir (= *S. caffrorum* Snowden). Note that race bicolor types should be regarded as co-dispersing along most, if not all trajectories, but these are only indicated where no advanced races are involved.

with wild *Sorghum propinquum*. The extent to which *S. propinquum* provided key adaptive attributes to cultivars requires genetic research, but it can be hypothesized to have contributed to race durra or to kaoliang sorghums (Snowden's *S. nervosum*) that extend north to c. 40° latitude in China, Korea and Japan.

The schema of sorghum dispersal and differentiation takes into account our current understanding of sorghum genetics, as well as available archaeobotanical finds, but also fits with several linguistic inferences. The later adoption of sorghum into established pearl millet farming systems across west Africa in the past 2000–2500 years is evident in linguistic evidence for a widespread cognate term for sorghum, “*kVn-*”, which seems to have spread as a loan across several distinct language families and subfamilies, including West/Central Afro-Asiatic, Songhay and Saharan and several subgroups of Niger-Congo (Mande, Atlantic, Adamawa, and some West Benue-Congo languages) (Blench 2006: 215), but apparently after Bantoid languages had already diverged and moved southward with a focus on rainforest subsistence (cf. Bostoen 2014). These more woodland-focused Bantu groups (Grollemund et al. 2015), picked up pearl millet by 2500 years ago, in keeping with traditions of food preparation that included a stiff porridge of a starchy staple and production of flour, and related cooking terms (Ricquier and Bosteen 2011). The lines of margaritifera guinea sorghums that gave rise to kafirs might also have moved via the same routes as pearl millet through the Congo, i.e. the Sangha River Interval, or, given the lack of archaeobotanical evidence, have diffused secondarily through these same societies after farming was already established, much as Asian cultivars probably did. Once established in southeast Africa, this lineage was carried via Indian Ocean trade to India to become Indian guineas. That these are popular in forested hill tracts through central and eastern India probably reflects the higher rainfall adaptations that ultimately derived from wild race arundinaceum, as well as their suitability to whole grain cooking as opposed to flour cuisine (Appa Rao et al. 1996).

As farmers of the eastern Bantu stream spread to the eastern/northeastern African rainforest margins, new cereals were incorporated into their subsistence, evident in loan words into the Eastern Bantu proto-language, or its early decedents, including a widespread pearl millet term (\*-*bedé*), most likely from Eastern Sudanic languages around the margins of what is today South Sudan or the Central Africa Republic (Ricquier and Bosteen 2011). Similarly, terms for sorghum (\*-*saka*; \*-*pemba*; \*-*pila*) were adopted into Eastern Bantu or some of its subgroups in the great lakes region of eastern Africa from Central Sudanic languages (Ehret 1973; cf. Philippson and Bahuchet 1994). This is congruent with sorghum, including both races bicolor and caudatum being adopted into eastern African agriculture in the early first millennium AD.

Thus the history of early agriculture in Africa is not merely a narrative of migrating farmers but also borrowing across ethnolinguistic groups and local adaptations in part arising from capturing genetic diversity from local wild sources. Some crop varieties moved long-distances, sometimes with highly mobile economies, like those posited for the Neolithic Sahel, but also sometimes via long-distance trade, around the Bronze Age Arabian sea and later Indian Ocean.

For most of Africa sorghum is central to agriculture, overlapping with and extending beyond the range of other African cereals. It has forms nearly as tolerant of low rainfall as pearl millet and others that, like finger millet, range into higher rainfall

and mountainous zones. Compared to both it is relatively more productive. In traditional East African agriculture, for example, sorghum yields from 550–1700 kg/ha, compared to 450–900 kg/ha for finger millet, and on average c. 450 kg/ha for pearl millet (Acland 1971), a range of 270–900 kg/ha is reported for West African pearl millet (Irvine 1969). Under rainfed cultivation African rice (*Oryza glaberrima*) yields 450–900 kg/ha, although 1000–3000 kg is reported for wet fields (Borlaug et al. 1996). In general then, sorghum is the most productive rainfed cereal in most African environments, at least prior to the introduction of American maize. Thus it is not surprising that sorghum cultivation is recurrently associated with sedentary farming and urbanisation in many different cultural traditions of pre-historic Africa, from the Inland Niger Delta (McIntosh 1995) to Meroitic Nubia (Fuller 2014), from Swahili islands (Boivin et al. 2013) to Engaruka (Sassoon 1967) and Great Zimbabwe (Chirikure et al. 2014); and it is unique amongst the African cereals in not just flourishing in similar environments in India but making inroads into northern temperate farming systems, in the Mediterranean or northeastern Asia.

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