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Author(s): J. M. J. de Wet
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SPECIAL PAPER

SYSTEMATICS AND EVOLUTION OF SORGHUM SECT. SORGHUM (GRAMINEAE)[1]

J. M. J. DE WET

Crop Evolution Laboratory, Department of Agronomy, University of Illinois, Urbana 61801

ABSTRACT

The genus *Sorghum* Moench is subdivided into sections *Chaeotosorghum*, *Heterosorghum*, *Parasorghum*, *Stiposorghum* and *Sorghum*. Section *Sorghum* includes two rhizomatous species, *S. halepense* (L.) Pers. ($2n = 40$) and *S. propinquum* (Kunth) Hitchcock ($2n = 20$), as well as the annual *S. bicolor* (L.) Moench ($2n = 20$). *Sorghum bicolor* is divided into subspecies *bicolor* to include all domesticated grain sorghums, subspecies *drummondii* (Steud.) de Wet comb. nov. to include stabilized derivatives of hybridization among grain sorghums and their closest wild relatives and subspecies *arundinaceum* (Desv.) de Wet et Harlan to include the wild progenitors of grain sorghums. Four ecotypes of subspecies *arundinaceum* are recognized: race aethiopicum of the arid African Sahel, race virgatum of northeastern Africa, race arundinaceum of the African tropical forest, and race verticilliflorum of the African Savanna. The numerous, usually recognized grain sorghums are divided among five basic races, bicolor, caudatum, durra, guinea and kafir, and ten hybrid races that each combine characteristics of at least two of these basic races. Races of grain sorghum are morphologically distinct, and they maintain their unity of type through spacial and ethnological isolation.

Sorghum Moench is a heterogeneous genus. The following sections are usually recognized: *Stiposorghum*, *Parasorghum*, *Sorghum*, *Heterosorghum* and *Chaetosorghum* (Garber, 1950). *Stiposorghum* and *Parasorghum* are characterized by distinct rings of hairs at each culm node, with the awns of *Stiposorghum* over 65 mm long and those of *Parasorghum* substantially shorter. The culm nodes are glabrous or hairy in *Sorghum*, *Chaetosorghum* and *Heterosorghum*, but never do the hairs form a nodal ring. The pedicellate spikelets are reduced to subequal glumes in *Heterosorghum* and unequal glumes in *Chaetosorghum*. Section *Sorghum* is characterized by better developed pedicellate spikelets that are often male fertile but almost always female sterile. Sessile spikelets in the genus *Sorghum* are bisexual.

Section *Sorghum* includes cultivated grain sorghum, a complex of closely related annual taxa from Africa, and a complex of perennial taxa from southern Europe and Asia. This section has received considerable attention from systematists (Snowden, 1936; 1955). As is true for most genera which include domesticated taxa, the genus is over classified. The perennial complex is usually recognized to include four species, spontaneous taxa are divided among 17 species, and Snowden (1936) recognized 31 domesticated species. Cultivated and spontaneous annual taxa are all interfertile, perennial polyploid taxa cross readily to produce fertile hybrids, and diploid perennial taxa are interfertile with all diploid annual taxa. This paper summarizes experimental data accumulated over two decades of biosystematic studies in *Sorghum*.

MATERIAL AND METHODS—Herbarium specimens and seed were collected across the range of section *Sorghum* in Europe, Africa and southern Asia. Plants were grown in uniform nurseries at Stillwater, Oklahoma, Mayagüez, Puerto Rico, and at Urbana, Illinois, for comparative morphological studies. Hybrids among taxa were produced following hand emasculation of individual spikelets. Chromosome number and behavior were studied in developing microsporocytes stained with acetocarmine. Statistical analyses of morphological data were presented in earlier publications by the author and his students. Herbarium specimens of all collections (over 5,000 specimens) are filed with the herbarium of the Crop Evolution Laboratory at the University of Illinois.

SYSTEMATICS—Section *Sorghum* is usually divided into two groups, the Halapensia complex and the Arundinacea complex. Snowden (1955) includes four rhizomatous species in the Halapensia—*S. controversum* (Steud.) Snowden, *S. halepense* (L.) Pers., *S. miliaceum* (Roxb.) Snowden, and *S. propinquum* (Kunth) Hitch-

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cock. The first mentioned three taxa are tetraploid ($2n = 40$). Cytologically they behave as autotetraploids, cross readily with one another, and hybrids among them in all possible combinations are as fertile as their parents. They evidently belong to one biological species. *Sorghum propinquum* is a diploid ($2n = 20$). Celarier (1958) suggested that *S. propinquum* is the diploid ancestor of the tetraploid rhizomatous taxa. However, comparative morphology refutes such an assumption. Harlan and de Wet (1972) proposed that this species belong with *S. bicolor* (L.) Moench because it crosses with grain sorghum to produce fertile hybrids.

The Arundinacea complex, as recognized by Snowden (1936; 1955), includes seven weedy species, 13 wild species and 28 species of cultivated grain sorghums. The grain sorghums are artifacts of human selection and cultivation (de Wet and Huckabay, 1967; de Wet, Harlan, and Price, 1976), and the different cultivated kinds deserve at most racial status (Harlan and de Wet, 1972). The wild and weedy taxa of the Arundinacea complex are all interfertile, and de Wet, Harlan, and Price (1970) demonstrated that hybridization among the four basic taxa, *S. arundinaceum* (Desv.) Stapf, *S. aethiopicum* (Hack.) Rupr. ex Stapf, *S. verticilliflorum* (Steud.) Stapf and *S. virgatum* (Hack.) Stapf, and hybridization of these with domesticated kinds, accounts for all the variability described by Snowden (1955) in the spontaneous groups of this complex. Evidently wild, weedy and cultivated taxa of the Arundinacea complex belong to one biological species.

Three species are recognized in section *Sorghum*, two rhizomatous taxa, *S. halepense* and *S. propinquum*, and the large and complex *S. bicolor* to include all annual wild, weedy and cultivated taxa.

1. *Sorghum halepense* (L.) Pers., Synops. 1, 101: 1805. Based on *Holcus halapensis* L., Sp. Pl. ed. 1, 1047. 1753. *S. miliaceum* (Roxb.) Snowden, J. Linn. Soc. Bot. 5: 205. 1955. Based on *Andropogon miliaceus* Roxb., Fl. Indica 1, 276. 1820. *S. controversum* (Steud.) Snowden, J. Linn. Soc. Bot. 55: 210. 1955. Based on *Andropogon controversus* Steud., Syn. Pl. Glum. 1, 391. 1854. Synonymy is discussed in detail by Snowden (1955).

Plants perennial with well developed creeping rhizomes. Culms slender to robust, erect, mostly simple, 0.5–3.5 m tall and up to 2 cm wide near the base. Leaf blades linear up to 90 cm long and 4 cm wide, more or less smooth. Sheaths essentially glabrous. Inflorescence a large and more or less open panicle 10–60 cm long and 5–25 cm wide, with the lower branches up to 8 cm long in small inflorescences and up to 25 cm long in large ones. Panicle branches slender, often somewhat pendulous, usually naked for 2–5 cm from the base, divided upward. Racemes fragile, 1–5 noded up to 2.5 cm long, pedicels densely ciliate. Sessile spikelets 4.0–6.5 mm long, more or less elliptic-lanceolate, almost glabrous to densely hairy, awned or awnless. Glumes coriaceous, lower 7–12-nerved, with the wings of the keels ending in minute teeth, forming with the pointed apex a 3-toothed tip; upper glume not 3-toothed. Lemmas ciliate, lower 3–5 mm long, upper 3–4 mm long, minutely bilobed with usually a 10–16 mm long awn. Stamens three. Grains oblong-ovate, 2–3 mm long. Pedicellate spikelets male or neuter, 4–7 mm long.

Sorghum halepense is a native of southern Eurasia east to India. Slender plants with relatively small inflorescences, and narrow leaf blades occupy the western range of the species. These specimens are commonly classified as *S. halepense* while more robust plants with large inflorescenses and broader leaf-blades, and which occupy the eastern half of the species range are usually recognized as *S. miliaceum*. The species has also been introduced as a weed to all warm temperate regions of the world. In the Americas it has introgressed with grain sorghum to produce the widely distributed Johnson grass (Celarier, 1958). In Argentina, derivatives of such introgression were described as *S. almum* Parodi (Parodi, 1943; Saez, 1949; Hadley, 1953).

2. *Sorghum propinquum* (Kunth) Hitchc., Lingnan Sci. J. 7: 249. 1929. Based on *Andropogon propinquus* Kunth, Rev. Gram. 1, Suppl. 40. 1830.

Plants robust, tufted, perennial with stout rhizomes. Culms up to 5 m tall, erect. Leaf blades linear, up to 1 m long and 3–5 cm wide. Leaf sheaths glabrous. Inflorescences large, open, up to 60 cm long, with slender branches, the lower ones up to 25 cm long, usually bare of spikelets for as much as 5 cm at the base. Racemes fragile, 1–5-noded, with slender and ciliated pedicels. Sessile spikelets elliptic-lanceolate, 3.5–5.0 mm long, strigose at the base and above the middle, usually awnless. Glumes crustaceous below and membranaceous near the tip, lower keeled, often ending in minute teeth, upper glume similarly keeled. Lemmas thinly ciliate above the middle, lower 3.5–4.5 mm long, upper one about 3 mm long, usually awnless. Anthers three. Grains obovate 1.5–2.0 mm long. Pedicellate spikelets 4.0–5.5 mm long, male, rarely neuter.

Sorghum propinquum occurs in Ceylon and southern India, and from Burma eastward to the islands of southeastern Asia. Specimens from the Southeast Asian islands usually have smaller (4.0–4.5 mm) sessile spikelets than collections

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from the South Asian mainland (4.5–5.0 mm). In the Philippines this species crosses with introduced grain sorghum, and derivatives of such crosses are obnoxious weeds in parts of Luzon and Mindanao islands.

Hybrids between *S. propinquum* and *S. bicolor* are fully fertile and these two taxa evidently belong genetically to one biological species. The natural distribution of *S. bicolor*, however, is strictly African, and since *S. propinquum* is spacially isolated from the annual *S. bicolor*, this perennial taxon is recognized as a species. Distribution and morphology indicate affinities with *S. halepense* rather than *S. bicolor*. Hybrids between *S. halepense* ($2n = 40$) and *S. propinquum* ($2n = 20$) are characterized by a substantial number of trivalent chromosome configurations during meiotic prophase of microsporogenesis. Cytological behavior is completely regular in hybrids between *S. propinquum* and *S. bicolor*.

3. *Sorghum bicolor* (L.) Moench, Meth. Pl. 207. 1974. Based on *Holcus bicolor* L., Mant. Alt. 301. 1771. The synonymy of this species is extensive and is fully discussed by Snowden (1936).

Plants annual, often tillering. Culms erect, slender to robust, 0.5 m to over 5 m tall, branched or unbranched at maturity. Leaf blades linear to linear-lanceolate, glabrous or hairy, up to 1 m long and 10 cm wide; sheaths glabrous to hirsute or pubescent. Inflorescence an open or contracted panicle, 5–50 cm long and 3–30 cm wide, with the branches stiffly ascending or spreading and sometimes pendulous and the lower panicle branches often about half as long as the panicle, usually bare for up to 10 cm from the insertion with the primary axis. Racemes fragile, tough or tardily disarticulating at maturity, one- to several-noded. Sessile spikelets elliptic-lanceolate to obovate, up to 6 mm long, glabrous to densely hirsute or pubescent. Glumes coriaceous to membranaceous, shorter than, as long as or longer than the spikelet, usually winged on the keels, sometimes three-toothed. Lemmas of sessile spikelets hyaline, moderately ciliate, lower up to 6 mm long, the upper one usually somewhat shorter, often awned. Anthers three. Sessile spikelets bisexual, pedicellate spikelets male or neuter.

The species *S. bicolor* includes all annual taxa of section *Sorghum* as recognized by Snowden (1936, 1955). It comprises an extremely variable complex of cultivated taxa, a widely distributed and ecologically variable wild African complex, and stabilized weedy derivatives derived from introgression between domesticated grain sorghums and their closest wild relatives. These three complexes are here recognized as subspecies.

3a. *Sorghum bicolor* subsp. *bicolor*. Based on *S. bicolor* (L.) Moench, Meth. Pl. 207. 1794. The species of grain sorghum recognized by Snowden are listed in alphabetical order for convenience.

Sorghum ankolib Stapf in Prain, Fl. Trop. Afr. 9: 135. 1917.
S. basutorum Snowden, Kew Bull. 1935: 232. 1935.
S. bicolor (L.) Moench, Meth. Pl. 207. 1794.
S. caffrorum Beauv., Agrost. 131, 178. 1812.
S. caudatum Stapf in Prain, Fl. Trop. Afr. 9: 131. 1917.
S. cernuum Host. Gram, Austr. 4, 2, t. 3. 1809.
S. conspicuum Snowden, Kew Bull. 1935: 226. 1935.
S. coriaceum Snowden, Kew Bull. 1935: 240. 1935.
S. dochna (Forrsk.) Snowden, Kew Bull. 1935: 234. 1935.
S. dulcicaule Snowden, Kew Bull. 1935: 247. 1935.
S. durra Stapf in Prain, Fl. Trop. Afr. 9: 129. 1917.
S. elegans (Koern.) Snowden, Kew Bull. 1935: 238. 1935.
S. exsertum Snowden, Kew Bull. 1935: 230, 1935.
S. gambicum Snowden, Kew Bull. 1935: 229. 1935.
S. guineense Stapf in Prain, Fl. Trop. Afr. 9: 123. 1917.
S. margaritiferum Stapf in Prain, Fl. Trop. Afr. 9: 125. 1917.
S. melaleucum Stapf in Prain, Fl. Trop. Afr. 9: 134. 1917.
S. mellitum Snowden, Kew Bull. 1935: 225. 1935.
S. membranaceum Chiov., Monogr. Rapp. Col. Rome 19: 23–34. 1912.
S. miliiforme (Hack.) Snowden, Kew Bull. 1935: 237. 1935.
S. nervosum Bess. ex Schult. in Roem., et Schult., Syst. Veg. 2, Mant. 669. 1827.
S. nigricans (Ruiz et Pavon) Snowden, Kew Bull. 1935: 244. 1935.
S. notabile Snowden, Kew Bull. 1935: 239. 1935.
R. rigidum Snowden, Kew Bull. 1935: 248. 1935.
S. roxburghii Stapf in Prain, Fl. Trop. Afr. 9: 126. 1917.
S. simulans Snowden, Kew Bull. 1935: 237. 1935.
S. splendidum (Hack.) Snowden, Kew Bull. 1935: 233. 1935.
S. subglabrescens Schweinf. et Aschers. in Schweinf., Beitr. Fl. Aethiop. 302, 306. 1867.

Synonymy of the various cultivated taxa is listed by Snowden (1936).

Plants annual, with stout clums up to 5 m tall,

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often branched, frequently tillering. Leaf blades up to 90 cm long and 12 cm wide, usually more or less glabrous. Sheaths glabrous or sparsely pilose. Inflorescence an open or contracted panicle, up to 60 cm long and 30 cm wide, branches often several from each of the lower nodes, obliquely ascending or spreading, slender and pendulous or stiff, the lower ones often almost as long as the panicle. Racemes tough, usually 1–5-noded. Sessile spikelets elliptic to oblong, extremely variable in size and shape usually 3.0–9.0 mm long and 2.0–5.0 mm wide at maturity, glabrous to pilose. Glumes equal to subequal, coriaceous to membranaceous, keeled, often terminating into three minute teeth. Lemmas finely ciliate, lower awnless, the upper often awned. Pedicellate spikelets linear-lanceolate, male or neuter, persistent or deciduous.

Cultivated grain sorghums were divided into the Guineensia, Nervosa, Bicoloria, Caffra and Durra complexes by Snowden (1936). These complexes each include related cultivars that were recognized as races by de Wet and Huckabay (1967). A detailed comparative morphological study of grain sorghums led Harlan and de Wet (1972) to recognize five basic races, and ten hybrid races that combine characteristics of any two or more basic races.

Race bicolor—This race is based on subseries Bicoloria of Snowden. It is characterized by open inflorescences and long clasping glumes that usually enclose the elliptic grain at maturity. Bicolor sorghums resemble spontaneous weedy sorghums, but they lack the ability of natural seed dispersal. Members of race bicolor, particularly those far removed from their African center of origin, probably represent relics of ancient cultivated kinds. Others may have originated as selections out of derivatives from hybridization between modern cultivated races and wild members of *S. bicolor*. Bicolor sorghums are low yielding as cereals. They are rarely an important crop, but are grown across the range of sorghum cultivation in Africa and Asia. Some selections are grown strictly for their sweet stems, while in Africa other kinds are grown for their bitter grains that are used to flavor sorghum beer. The race is morphologically heterogeneous. It includes *S. dochna* and *S. bicolor* of the Bicoloria, *S. exsertum* of Guineensia, and *S. splendidum* and *S. nervosum* of the Nervosum subseries.

Race kafir—This race is based on subseries Caffra of Snowden with *S. caudatum* omitted. It is characterized by more or less compact inflorescences that are often cylindrical in outline. Sessile spikelets are typically elliptic with the glumes, at maturity, tightly clasping the usually much longer grain. The name is derived from 'kafir' the Arabic for unbeliever, referring to the Bantu who grow this race. Kafir sorghums are important staples across the eastern and southern savanna from Tanzania to South Africa. The race includes *S. caffrorum* and *S. coriaceum*.

Race caudatum—This race is based on *S. caudatum* and *S. nigricans* of subseries Caffra. caudatum sorghums have characteristic turtle-backed grains that are flat on one side and distinctly curved on the opposite side. The grains are usually exposed between the shorter glumes at maturity. The inflorescences range in shape from compact to open. This race is closely associated with speakers of Chari-Nile languages in Africa (Stemler, Harlan, and de Wet, 1975). It is widely grown in Chad, Sudan, northeastern Nigeria and Uganda. It is an old race of grain sorghum. Carbonized grains from Daima, dated to the ninth century (Connah, 1967), belong typically with race caudatum.

Race durra—This race includes *S. durra* and *S. cernuum* of subseries Durra. The name is derived from the Arabic name for sorghum, and the distribution of race durra is closely associated with Islamic people in Africa. Inflorescences are usually compact. Sessile spikelets are characteristically flattened and ovate in outline, and the lower glume is creased near the middle or with the tip a distinctly different texture than the lower two-thirds. Durra sorghums are widely grown along the fringes of the southern sahara, across arid West Africa, the Near East and parts of India. A sheath of sorghum discovered in a building at Qasr Ibrim and dated to Meroitic time (Plumley, 1970) is composed of durra-like sorghums.

Race guinea—This race is based on subseries Guineensia. It is characterized by long and gaping glumes that reveal the obliquely twisted grain at maturity. Inflorescences are usually large and open, with the branches often pendulous at maturity. The race is primarily a sorghum of West Africa, but is also grown along the East African rift from Malawi south to Swaziland. Some cultivars are adapted for cultivation in high rainfall areas, and others are used in décrue agriculture (Harlan and Pasquereau, 1969). Guinea sorghums are grown extensively in northern Nigeria where hybridization with drought-tolerant kinds of race durra is evident. Race guinea includes three well defined cultivated groups (de Wet, Harlan, and Kurmarohita, 1972). The one complex includes *S. margaritiferum* with its varieties, and is characterized by small (3.0–5.0 mm long) grains that are shorter than the glumes. This complex is grown in the high rainfall areas of West Africa and the fog-belt of eastern South

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Africa. In West Africa the flinty grains are cooked and eaten as rice. The Snowdenian *S. guineense*, *S. conspicum* and *S. gambicum* have larger (5.0–9.0 mm long) grains that are about equal in length to the gaping glumes. This complex is widely grown in the broad leaf savanna of West Africa, and the savanna of Malawi. In Malawi the inflorescences are often picked before they mature, and the sweet grains are eaten raw after drying. *Sorghum roxburghii* is intermediate in spikelet morphology between races guinea and kafir. This complex extends across the range of sorghum cultivation in Africa and South Asia.

Intermediate races—Besides *S. roxburghii*, several other Snowdenian species do not typically belong with any one of the five basic races. *Sorghum ankolib*, *S. rigidum* and *S. subglabrescens* are intermediate in spikelet morphology between races bicolor and durra. Derivatives of hybridization between races guinea and caudatum are represented by *S. dulcicaule* and some varieties of *S. elegans* and *S. notabile*. *Sorghum melaleucum* and *S. mellitum* are guinea-bicolor in spikelet morphology, and the intermediate kafir-bicolor complex includes *S. basutorum*, *S. miliiforme*, *S. simulans* and some cultivars of *S. elegans* and *S. nervosum*. Some cultivars of *S. nigricans* as recognized by Snowden are derivatives of kafir-caudatum hybridization. Hybrid races occur primarily where two or more basic races overlap. However, the hybrid morphology of some intermediate races has become fixed and several of these kinds are grown beyond their probable centers of origin.

3b. *Sorghum bicolor* subsp. *drummondii* (Steud.) de Wet, comb. nov. Based on *S. drummondii* (Steud.) Millsp. et Chase, Publ. Field Columb. Mus. Bot. 3: 21. 1903. The species of weedy sorghums recognized by Snowden are listed in alphabetical order.

Sorghum atterimum Stapf in Prain, Fl. Trop. Afr. 9: 121. 1917.
S. drummondii (Steud.) Millsp. et Chase, Publ. Field Columb. Mus. Bot. 3: 21. 1903.
S. elliotii Stapf in Prain, Fl. Trop. Afr. 9: 118. 1917.
S. hewisonii (Piper) Longley, J. Agric. Res. 44: 318, 319. 1932.
S. niloticum (Stapf ex Piper) Snowden, J. Linn. Soc. Bot. 55: 258. 1955.
S. nitens (Busse et Pilger) Snowden, Kew Bull. 1935: 224. 1935.
S. sudanense (Piper) Stapf in Prain, Fl. Trop. Afr. 9: 113. 1917.

Synonymy of these taxa is listed by Snowden (1936, 1955).

Plants annual with relatively stout culms up to 4 m tall. Leaf blades lanceolate, up to 50 cm long and 6 cm wide. Panicle variable, usually rather contracted, sometimes similar to that of the cultivated grain sorghum this subspecies accompanies as a weed, up to 30 cm long and 15 cm wide, branches often somewhat pendulous. Racemes more or less crowded, mostly 3–5-noded, tardily disarticulating at maturity. Sessile spikelets lanceolate-elliptic, 5–6 mm long. Lemmas hyaline, ciliate, lower around 6 mm, upper around 5 mm in length, shortly lobed, and the lower often awned. Grains variable, usually somewhat resembling the shape of the grain of the cultivated race from which the weed was derived. Pedicellate spikelets male or neuter.

Subspecies *drummondii* occurs as a weed in Africa wherever cultivated grain sorghums and their closest wild relatives are sympatric. All races of subspecies *bicolor* and all wild kinds of *S. bicolor* hybridize to produce weedy derivatives. Morphologically stabilized derivatives often accompany grain sorghums as weeds beyond the natural range of *S. bicolor*. These occur widely in India and the highlands of Ethiopia. Grain sorghums also introgress with the widely distributed Eurasian tetraploid *S. halepense* in South Asia, and in other parts of the world where this rhizomatous perennial became established, to form both annual diploid and perennial tetraploid weedy derivatives. The widely distributed chicken corn of the southeastern United States probably originated from an abandoned cultivated grain sorghum. It is characterized by fragile racemes, but disarticulation takes place by breaking of the rachis, rather than through callus formation as is typical for spontaneous sorghum. Weeds with similar dispersal mechanisms were collected among sorghum plants in Africa outside the range of wild *S. bicolor*, and in the Punjab.

3c. *Sorghum bicolor* subsp. *arundinaceum* (Desv.) de Wet et Harlan in Harlan, de Wet et Stemler, Origins Afr. Plt. Dom. 455. 1976. Based on *S. arundinaceum* (Desv.) Stapf in Prain, Fl. Trop. Afr. 9: 119. 1917. The species of wild sorghums usually recognized are listed alphabetically.

Sorghum arundinaceum (Desv.) Stapf in Prain, Fl. Trop. Afr. 9: 114. 1917.
S. aethiopicum (Hack.) Rupr. ex Stapf in Prain, Fl. Trop. Afr. 9: 119. 1917.
S. brevicarinatum Snowden, J. Linn. Soc. Bot. 55: 242. 1955.
S. castaneum Hubb. et Snowden, Kew Bull. 1936: 316. 1936.
S. lanceolatum Stapf in Prain, Fl. Trop. Afr. 9: 112. 1917.

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S. macrochaeta Snowden, Cult. Races Sorgh. 237. 1936.
S. panicoides Stapf in Prain, Fl. Trop. Afr. 9: 120. 1917.
S. pugionifolium Snowden, J. Linn. Soc. Bot. 55: 240. 1955.
S. somaliense Snowden, J. Linn. Soc. Bot. 55: 238. 1955.
S. usumbarense Snowden, J. Linn. Soc. Bot. 55: 238. 1955.
S. verticilliflorum (Steud.) Stapf in Prain, Fl. Trop. Afr. 9: 116. 1917.
S. virgatum (Hack.) Stapf in Prain, Fl. Trop. Afr. 9: 111. 1917.
S. vogelianum (Piper) Stapf in Prain, Fl. Trop. Afr. 9: 116. 1971.

Synonymy is discussed in detail by Snowden (1955).

Plants tufted annuals or weak biannuals, with slender to stout culms that may reach 4 m in height. Leaf blades linear-lanceolate to 75 cm long and 7 cm wide. Panicles usually large, somewhat contracted to loose, up to 60 cm long and 25 cm wide, with the branches obliquely ascending or spreading, sometimes pendulous. Racemes 1–5-noded, fragile. Sessile spikelets lanceolate to elliptic, 5–8 mm long, usually ciliate. Glumes coriaceous, more or less ciliolate at least in the upper third. Lemmas ciliate, lower up to 7 mm, upper around 5 mm long, 2-lobed, the upper awned from between the lobes, rarely awnless. Grains lanceolate to obovate-lanceolate. Pedicelled spikelets male or neuter often longer than the sessile spikelet.

Subspecies *arundinaceum* was divided among three varieties by de Wet and Huckabay (1967), and a fourth variety was added by de Wet, Harlan, and Price (1970). These varieties, however, grade morphologically and ecologically so completely into one another that they do not deserve formal taxonomic status. They are more or less well defined ecotypes. The widest distributed and morphologically most variable is race verticilliflorum. It extends across the African savanna and was introduced to tropical Australia, parts of India and the New World. Race verticilliflorum can be distinguished from other wild sorghums by its large and open inflorescences with spreading, but not pendulous branches. This race grades into race arundinaceum which is distributed across tropical Africa as a forest grass. In the broad leaf savanna race arundinaceum is often difficult to distinguish from race verticilliflorum except by inflorescences in which the branches become pendulous at maturity. Race virgatum resembles race verticilliflorum except that the inflorescence branches are more erect, and the leaf blades are narrowly linear. Race virgatum occurs along streambanks and irrigation ditches in arid northeastern Africa. Race aethiopicum is a desert grass, and is easily recognized by its large ovate-lanceolate, densely tomentose sessile spikelets. It occurs across the Sahel from Mauritania to the Sudan.

EVOLUTIONARY DYNAMICS OF SORGHUM DOMESTICATION—Domesticated grain sorghums originated from wild members of *S. bicolor* subsp. *arundinaceum* that were brought into cultivation. Snowden (1936), Portéres (1962) and de Wet and Huckabay (1967) suggested that races arundinaceum, aethiopicum and verticilliflorum could have independently given rise under domestication to guinea sorghums, durra sorghums and kafir sorghums, respectively. Doggett (1965) and de Wet and Harlan (1971), however, demonstrated that the earliest domesticated sorghums were bicolor-like, and that the modern domesticated races were derived from bicolor sorghums after the initial domestication. Morphological affinities between guinea sorghums and race arundinaceum, durra sorghums and race aethiopicum, and between kafir sorghums and race verticilliflorum can be explained on the basis that gene exchange occurs across weed races belonging to subspecies *drummondii*. Distribution of related wild and cultivated races coincide in Africa, and hybridization between sympatric wild and cultivated kinds commonly takes place. Harlan (1971) proposed that sorghum was first taken into cultivation along a broad band of the savanna between the Sudan and Nigeria. In this region race verticilliflorum is an abundant wild grass and is collected as a wild cereal in times of scarcity. From this region the cultivation of sorghum spread into tropical West Africa, the arid northeast and southeastern Africa. Selection for adaptation to a wet tropical habitat produced race guinea (de Wet, Harlan, and Kurmarohita, 1972). This migration probably occurred before 3,000 B.P. (Harlan and Stemler, 1976). After race guinea was well differentiated it spread to Malawi and later to southern Africa along the mountains of eastern Africa. Migration of bicolor sorghums south from the West African savanna probably occurred early in the history of sorghum domestication and race kafir may have originated from race bicolor south of the equator (de Wet and Harlan, 1971). However, Schechter and de Wet (1975) demonstrated closer genetic affinities between kafir sorghums and local wild kinds of race verticilliflorum than between race kafir and the other domesticated grain sorghums. This suggests an independent domestication of sorghum in the southeastern savanna. Caudatum sorghums are more or less limited to the original regions of bicolor domestication. This race was developed by speakers of present

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day Chari-Nile languages (Stemler, Harlan, and de Wet, 1975a). Durra sorghums probably originated outside Africa from bicolor sorghums that were introduced to the Sind-Punjab region of northwestern India some 3,000 years ago (de Wet and Huckabay, 1967; Harlan and Stemler, 1976). Race durra was later introduced into North and West Africa during the Islamic expansion across the Sahel and West African savanna, and later also became widely introduced into Ethiopia (Stemler, Harlan, and de Wet, 1975b).

Domestication of sorghum involved adaptation to the man-made habitat and adaptation beyond the original area of cultivation (de Wet, 1975). Racial evolution of grain sorghums is closely associated with ethnological, ecological and geographical isolation. Variation within races is determined by conscious selection for particular uses, and to satisfy the individual fancies of cultivators. Modern evolutionary development is accelerated by movement of cultivated kinds across previous isolating barriers. Experimentally produced cultivars are replacing traditional cultivars in many parts of Africa.

ANTIQUITY OF SORGHUM DOMESTICATION—It is not known when *Sorghum bicolor* was first brought into cultivation. Murdock (1959) proposes that this cereal, as well as several other West African crops were domesticated some 7,000 years ago. Doggett (1965) suggests that domestication took place somewhere in the northeastern quadrant of Africa some 5,000 years ago. Sorghum must have been domesticated in the savanna zone south of the Sahara, and certainly more than 3,000 B.P. (Harlan, 1971; Harlan and Stemler, 1976). However, conclusive evidence of the early evolutionary history of sorghum is lacking. Identifiable remains of cultivated sorghum in Africa date back only to the early centuries of the Christian era. Plumley (1970) discovered a beautifully preserved sheath of durra sorghum at Qasr Ibrim dating back to Meroitic times. Clark and Stemler (1975) identified bicolor sorghum from Jebel et Tomat in the Sudan (ca. 245 A.D.). Caudatum sorghum dated to the ninth century A.D., were found at Daima by Connah (1967). Cultivated sorghum, probably belonging to race guinea, was abundant at Muramasapwa in Malawi during the ninth century A.D. (Robinson, 1966), and kafir sorghums are commonly associated with early iron-age Bantu dwellings across southern Africa (Fouche, 1937; Summers, 1958; Fagan, 1967; Phillipson and Fagan, 1969; Shaw, 1976). Sorghum domestication certainly began earlier than these dates would suggest. During the beginning of the Christian era, modern races were already well established and, except for race durra, were probably widely distributed across their present ranges.

Evidence of early sorghum cultivation in Africa and India is often cited, but the data on which these conclusions are based are at best circumstantial. Clark (1971) cited a pottery impression of a single grain of sorghum from Adrar Bous in the Ari region of the Sahara dated to around 2,000 B.C. and Vishnu-Mittre (1974) cites several pottery impressions from Ahar in Rajasthan (ca. 1727 B.C.) that were identified as representing grains of sorghum. From Mohenjo-Daro, Marshall (1931) identified a drawing on a potsherd as that of sorghum (Vishnu-Mittre, 1974). These crude drawings, however, do not represent sorghum (see Marshall, 1931; Plate LXXXVII, fig. 5; LXXXVIII, fig. 2; XCII, fig. 5). Crops are often difficult to identify from early illustrations even by botanists. The often cited carved reliefs from the palace of Sennacherib at Ninevah are often cited as depicting sorghum plants (Piedallu, 1923; Hall, 1928, Plates 30, 32). However, the plants actually represent the common reed *Phragmites*. The plants illustrated grow along the edge of a marsh with pigs grazing among them, certainly not a habitat for cultivated sorghum. Similar plants are illustrated on imperial Sassanian hunting scenes from Iran (see Reed, 1965 for illustrations), where they are always shown to grow in marshes.

Sorghum domestication probably dates back to the advent of agriculture in subsaharan Africa (see Clark, 1976). Harlan and Stemler (1976) suggest that domestication took place before 3,000 B.P. and that cultivated sorghum reached northwestern India during the latter part of the second millennium B.C. Other African cereals, *Pennisetum americanum* (L.) Leeke (pearl millet), and possibly *Eleusine coracana* (L.) Gaertner (finger millet) were well established as crops in the Sind-Punjab region of India by 1000 B.C. (Vishnu-Mittre, 1974). From northwestern India the crop must have been introduced to China. The report of Ho (1969) that sorghum was discovered from a Yang-Shao site in southern Shansi province is probably based on mis-identification. This cereal became an important crop in China only after the Mongol conquest (Hagerty, 1940). Since the fifteenth century sorghum has also been widely introduced into the New World and during the last several decades has become an important crop in the U.S. and Mexico.

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