

Domestication of *Eleusine coracana*

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Eleusine coracana (L.) Gaertn. (finger millet or eleusine) is an important cereal in Africa and India. It is used in the production of beer, porridge, soup, bread, cake, and puddings. It is also one ingredient in the distilled liquor called "Arak" or "Arake". Flour of malted grain is used in India as food for infants and invalids, and is often fed to diabetic patients (Bhatnagar, 1952). Finger millet is also used as a prophylaxis for dysentery (Lemordant, 1967).

The cultivation and diversity of *E. coracana* in Africa as well as India led to considerable controversy over the time and place of its domestication, and as to its progenitor. De Candolle (1886) considered finger millet to be an Indian domesticate. He indicated that there are more species of *Eleusine* in the south of Asia than in any other part of the world, and that the crop has a Sanskrit but no Arabic name. Wildeman (1940) also believed that *E. coracana* is of Indian origin, and that it was later introduced into East Africa. He suggested that the crop subsequently moved to West Africa since here it is of minor importance. Because of its long history and morphological diversity in India, Greenway (1945) concluded that finger millet was domesticated there from the weedy *E. indica* (L.) Gaertn. Cobley (1956) also assumed that finger millet is of Indian origin, since several wild species are common there. Vishnu-Mittre (1968) identified carbonized *E. indica* and *E. coracana* grains from India, and dated them to around 1800 B.C. Hutchinson commented in the Vishnu-Mittre paper (1968) that the presence of *E. indica*

in Africa is doubtful and that the carbonized material of these two species in India is of particular importance for determining the place of origin of finger millet. This archaeological material, however, later proved to be not of *Eleusine*. On the basis of morphological evidence Porteres (1951, 1958, 1970) and Mehra (1963) considered finger millet to be an African domesticate, and Vavilov (1951) believed that finger millet could have originated independently in India and Africa. Not only the area of domestication of *E. coracana* is in question, but also its putative ancestor is not known with certainty. Kennedy-O'Byrne (1957) and Jameson (1970) suggested that *E. indica* and *E. africana* Kennedy-O'Byrne gave rise independently to Indian and African cultivars, while Mehra (1963) proposed that *E. africana* is wild finger millet.

Since archaeological evidence of *E. coracana* domestication is limited and inconclusive, evidence from comparative morphology, cytogenetics, distribution, and history have been collected in an effort to determine the origin and evolution of this crop.

MATERIALS AND METHODS

For comparative morphological studies, 200 seed collections of *E. coracana*, *E. africana*, and *E. indica* maintained by the USDA, and another 50 collections gathered in Africa and India by J. R. Harlan and J. M. J. de Wet of the Crop Evolution Laboratory, were grown in uniform nurseries at the University of Illinois. Herbarium specimens, indicating place of origin of all of these collections are filed in the herbarium of the Crop Evolution Laboratory (CEL). Ten specimens of each collection were used for comparative morphological studies. Chromosome numbers were determined from developing microspore

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Work supported by Ministry of Education and Higher Studies, Iraqi Government, and the Illinois Agricultural Experiment Station.

Submitted for publication September 30, 1974; accepted for publication November 8, 1974.

mother cells stained with aceto-carmin. Cluster analysis was performed for the eleven species of *Eleusine* and for the genus *Dactyloctenium*. Thirty-seven characters were used for statistical analysis. Twenty-five were floral and seed characters and the others referred to vegetative traits. For clustering analysis the condensed variant was calculated by using the formula $\bar{X}_{ij} = \{X_{ij} - \min(X_i)\} / \{\max(X_i) - \min(X_i)\}$. The *Q*-correlation coefficients were calculated for each of the 12 pairs of taxa according to Sokal and Sneath (1963). Clustering was done with the unweighted pair group method using simple averages.

Distribution maps are based on our herbarium collections (CEL), and specimens in the Royal Botanical Gardens at Kew, the Museum of Natural History in Paris, and the Botanical Museum in Berlin (see Phillips, 1972). Each dot on the maps represents one to several of these collections.

Grains of *E. coracana*, *E. indica*, and *E. africana* were carbonized in our laboratory for comparison with archaeological *Eleusine* collections. Grains were covered with sand, enclosed in aluminum foil and charred over a Bunsen burner.

Eleusine Gaertn. is a member of the tribe Chlorideae, and allied to the genera *Acrachne* Weight and Arn., and *Dactyloctenium* Willd. The genus includes eleven species. One, *E. tristachya* (Lam.) Lam. is widely distributed in South America; the other ten are Old World species, with *E. indica* widely naturalized as a weed also in the New World. Phillips (1972) excluded *E. compressa* (Forssk.) Christ. from *Eleusine*. This species differs from other members of the genus in its stoloniferous habit, and in spikelets which articulate from the top of the rachis. The other *Eleusine* species were subdivided by Phillips (1972) into two complexes on the basis of annual (*E. coracana*, *E. indica* subsp. *indica*, *E. indica* subsp. *africana*, and *E. multiflora* Hochst. ex A. Rich.), or perennial habit (*E. floccifolia* (Forssk.) Spreng, *E. intermedia* (Chiov.) Phillips, *E. jaegeri* Pilger, *E. kigeziensis* Phillips, and *E. semisterilis* Phillips). She indicated that within groups differences between species are small, and that natural hybridization among annuals often renders classification almost impossible

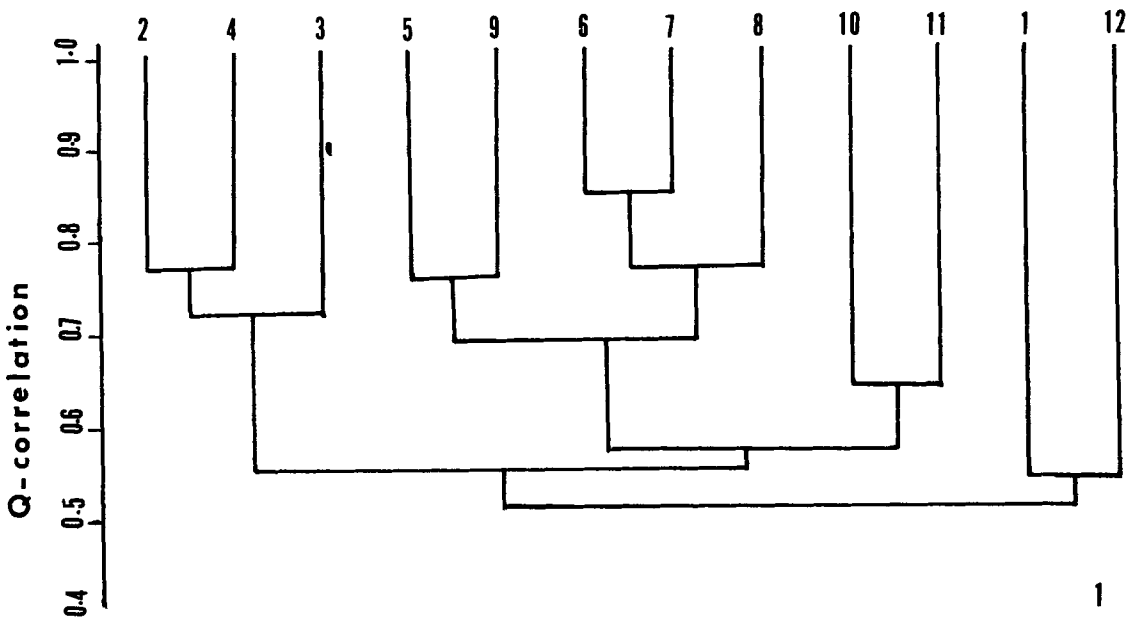


Fig. 1. Cluster analysis of *E. multiflora* (1), *E. coracana* (2), *E. indica* (3), *E. africana* (4), *E. semisterilis* (5), *E. floccifolia* (6), *E. kigeziensis* (7), *E. jaegeri* (8), *E. intermedia* (9), *E. tristachya* (10), *E. compressa* (11), and *Dactyloctenium* (12).

TABLE I
MORPHOLOGICAL COMPARISON OF FINGER MILLET AND ITS RELATIVES

Character	<i>E. coracana</i>	<i>E. africana</i>	<i>E. indica</i>
Culms	Robust	Robust	Slender
Spike width	8-15 mm	4-8 mm	3-5.5 mm
Spikelet articulation	Absent	Present	Present
Spikelet length	5-8 mm	4-8 mm	3-5 mm
Lemma length	2.2-4.7 mm	3.3-4.8 mm	2.1-2.8 mm
Grain length	1.2-1.8 mm	1.2-1.6 mm	1.0-1.3 mm
Grain surface	Granulated	Shallowly ridged	Obliquely striated

Cluster analysis of the eleven species of *Eleusine* (Fig. 1) revealed three major complexes in the genus. The elements of the first complex are *E. coracana*, *E. africana*, and *E. indica*. Within this complex, *E. coracana* is tightly clustered with *E. africana*. The second complex includes five species and could be split into two sub-complexes with *E. semisterilis* and *E. intermedia* representing one and *E. jaegeri*, *E. kigeziensis*, and *E. floccifolia* the other sub-complex. The third complex, which is not very tightly clustered with the other two, is made

up of *E. compressa* and *E. tristachya*. *Eleusine multiflora* clustered with *Dactyloctenium*, with a low Q-correlation. *Eleusine multiflora* differs from the other members of *Eleusine* by the mucronate lemma, deciduous pericarp, and occasionally the way of floret disarticulation (Phillips, 1972).

The genus *Eleusine* was studied cytogenetically by Chennaveeraiah and Hiremath (1974). *Eleusine compressa* ($2n = 40$) and *E. jaegeri* ($2n = 20$) were found to have a basic chromosome number of $x = 10$; *E. multiflora* ($2n = 16$) is a diploid

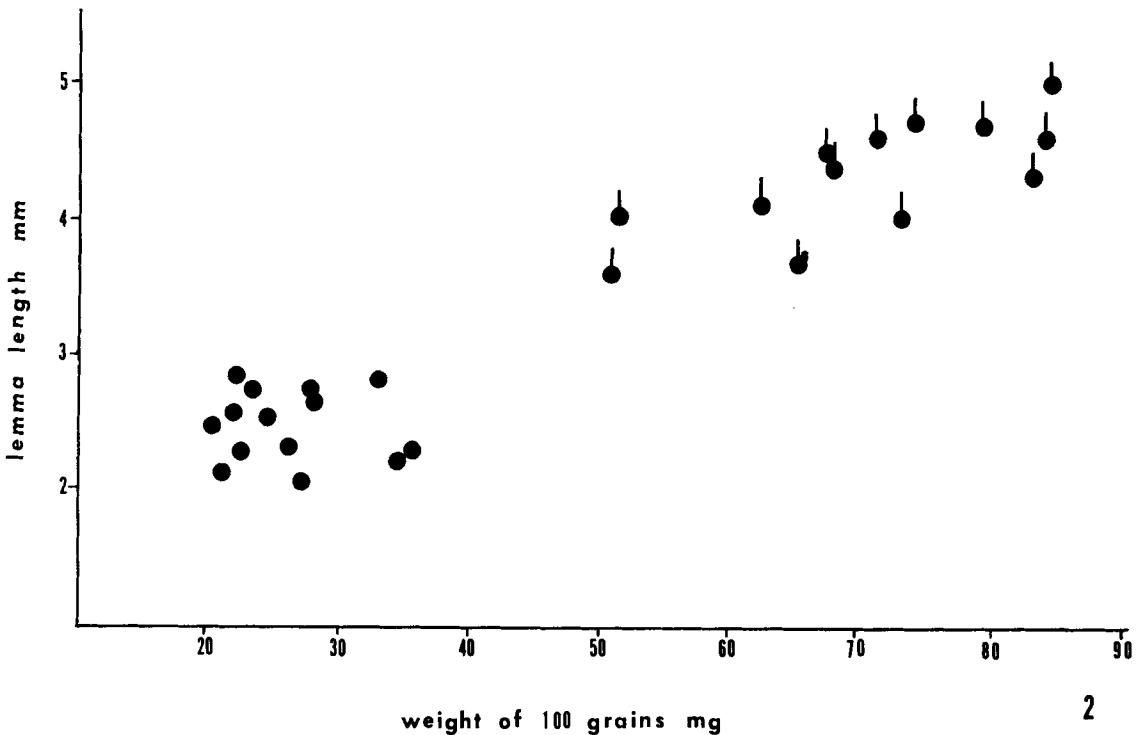


Fig. 2. Scatter diagram showing the significance of grain weight, lemma length, and glumes length in the separation of *E. indica* (lower left) and *E. africana* (upper right).
●: glumes length 2.1-2.8 mm ◐: glumes length 3.3-4.8 mm.



Fig. 3. African distribution of *E. africana* (solid circles ●), *E. indica* (open circles ○), and *E. coracana* (parallel lines ≡).

based on $x = 8$; *E. africana* ($2n = 36$), *E. floccifolia* ($2n = 18, 36$), *E. indica* ($2n = 18$) and *E. tristachya* ($2n = 18, 16$) are diploids and tetraploids based on $x = 9$; and *E. intermedia* and *E. kigeziensis* are unknown cytogenetically. Hybrids between *E. coracana* and *E. africana* are readily produced and are fully fertile. Mehra (1962) demonstrated that natural hybridization between these two taxa takes place in Ethiopia. Hybrids between *E. coracana* and *E. indica* can be produced, but these triploids are sterile with little evidence of homology between the parental genomes. Jameson (1940) collected sterile specimens in Uganda which he considered to represent hybrids between *E. coracana* and *E. indica*. Chennaveeraiah and Hiremath (1974) crossed *E. tristachya* and *E. africana* with *E. floccifolia*, obtaining sterile hybrids. Other crosses so far attempted have failed.

The cultivated *E. coracana* is morphologically allied to both *E. africana* and *E. indica* (Fig. 1). Phillips (1972) retained *E.*

coracana as a species, but combined *E. africana* with *E. indica* as a subspecies. Domesticated *E. coracana* differs morphologically from its closest wild relatives in the characters summarized in Table I. *Eleusine indica* and *E. africana* are readily separated when lemma length is plotted against grain length or weight (Fig. 2). *Eleusine africana* is not a subspecies of *E. indica* as proposed by Phillips (1972). It is cytogenetically conspecific with *E. coracana*, and genetically isolated from *E. indica*. Following Harlan and de Wet (1971) *E. coracana* is recognized to include all cultivated grain eleusine, and spontaneous races are included in *E. coracana* subsp. *africana* (Kennedy-O'Byrne) Hilu and de Wet (Comb. et stat. nov.). *Eleusine africana* was originally described by Kennedy-O'Byrne (1957) to separate robust African specimens from the smaller widely distributed *E. indica*. Subspecies *africana* is widely distributed in Africa (Fig. 3), but confined mainly to the uplands of eastern and

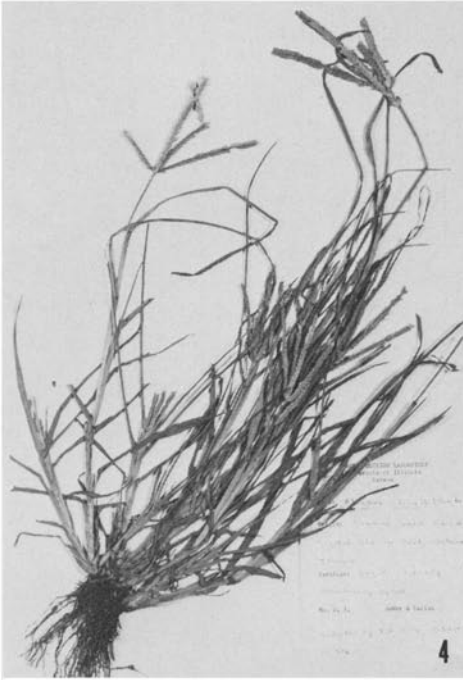


Fig. 4. *Eleusine indica*.

Fig. 5. Wild race of *E. coracana* subsp. *africana*.

Fig. 6. The weedy race Africana of *E. coracana* subsp. *africana*.

Fig. 7. The weedy race Dedza of *E. coracana* subsp. *africana*.

southern Africa. In contrast, *E. indica* (Fig. 4) occurs in Africa mainly along the eastern coast and along the inland lakes.

Three morphologically distinct races of subspecies *africana* are recognized; wild kinds and two weedy kinds which incorporate characteristics from the cultivated subspecies. Subspecies *africana* is a tufted annual with geniculately ascending culms up to 90 cm long that frequently root and branch from the lower nodes. The wild race is further characterized by spikes that usually are 4–12 cm long and 4–6 mm wide, and spikelets that are loosely arranged on the spikes (Fig. 5). The weedy races are usually more robust than the wild race, with spikes that are 10–17 cm long and 5–8 mm wide, and spikelets that are as closely packed on the spikes as those of subsp. *coracana*. The two weedy races will be referred to for convenience as *Africana* and *Dedza*. They differ in inflorescence structure. The inflorescences of race *Africana* (Fig. 6) are digitate, and composed of 3–15 ascending spikes arranged alternately or in whorls at the top of a primary axis, with usually 1–10 spikes located some distance below this main cluster. Race *Dedza* (Fig. 7) is characterized by inflorescences with a terminal spike having loosely packed spikelets, and below this, up to 15 subterminal spikes more or less digitately arranged along a short central axis. This latter race has so far been collected from *Dedza* and *Kota Kota* in Malawi and from *Iringa District* in Tanzania while the common weedy race occurs wherever wild and cultivated *E. coracana* are sympatric in Africa.

Eleusine coracana subsp. *coracana* is widely cultivated in Africa (Fig. 3) and India (Fig. 11). It is also cultivated in Burma, the southern parts of Tibet, Nepal, Malaysia, Sumatra, Sri Lanka, Philippines, Indochina, Japan, and China (Porteres, 1951), Java (Baker and Brink, 1968), Iran and Afghanistan (Rechinger, 1970), and in the Arabian Peninsula along the Red Sea and the Indian Ocean (Schwartz, 1939).

Subspecies *coracana* was recognized by Linnaeus (1759) as a member of *Cynosurus*, and based on an illustration by Plukenet (1691). Forms with finely striated grains are sometimes recognized as *E. tozusa* Fresen.

This species was reduced to a variety of *E. coracana* by Franchet (1895). Plants with straight ascending spikes are sometimes referred to as *E. stricta* (Roxburgh, 1814). This species is recognized as a variety of *E. coracana* by Nees von Eseneck (1841). Koernicke and Werner (1885) recognized *E. coracana* var. *genuina* to include cultivated kinds with curved spikes, and varieties *atra*, *fusca*, and *alba* to include kinds with straight spikes having black, red-brown, or white-yellow grains respectively. Grain color is not correlated with geographic distribution, has no ethnic unity, and consequently is a poor criterion on which to base racial differentiation. Growth habit and inflorescence morphology are more uniform in geographic areas, are commonly used by cultivators to distinguish domesticated kinds, and we consequently base our racial classification on these characters.

Subspecies *coracana* is characterized by erect to ascending stems that are up to 170 cm long, and usually tiller at the base. Degree of tillering varies among different kinds in uniform nurseries. Two or more adjacent internodes are often very short with the result that their branches cluster at one spot and, misleadingly, the branches appear to be opposite on one node. The inflorescence displays a great deal of variation in shape, but in general is digitate, and composed of spikes which are frequently subtended by lateral ones. Three basic types of inflorescence morphology are recognized in finger millet. Open types have straight and loose spikes (Fig. 10), top-curved types have the last 1–2 cm of the spikes recovered (Fig. 8), and in-curved types have the spikes of the inflorescence curved along their whole length (Fig. 9). Number of primary inflorescence branches varies from 4–26, and are equal or unequal in length in all three kinds. Below the main group of spikes, 0–7 additional spikes are usually clustered together. Spikes are 3.5–14 cm long, unbranched or with as many as 10 branches. Spikelets are 6–9 flowered, and 5–8 mm long. Glumes are unequal, and with a winged keel along the outer surface. The lower glumes are three-nerved and 1.5–3.0 mm long, while the upper glumes have 3–7

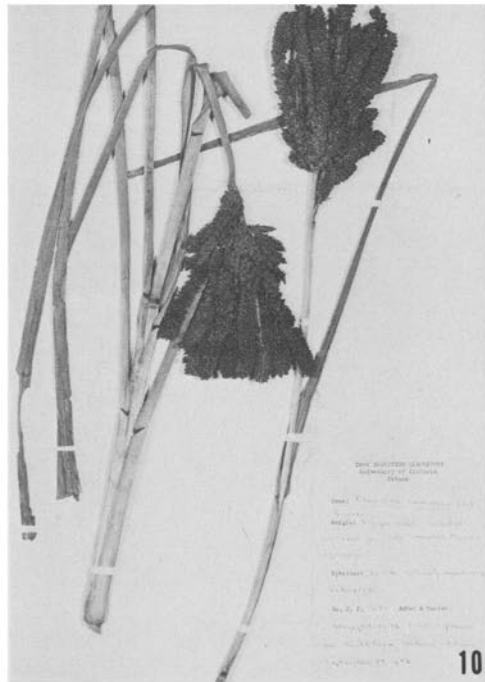
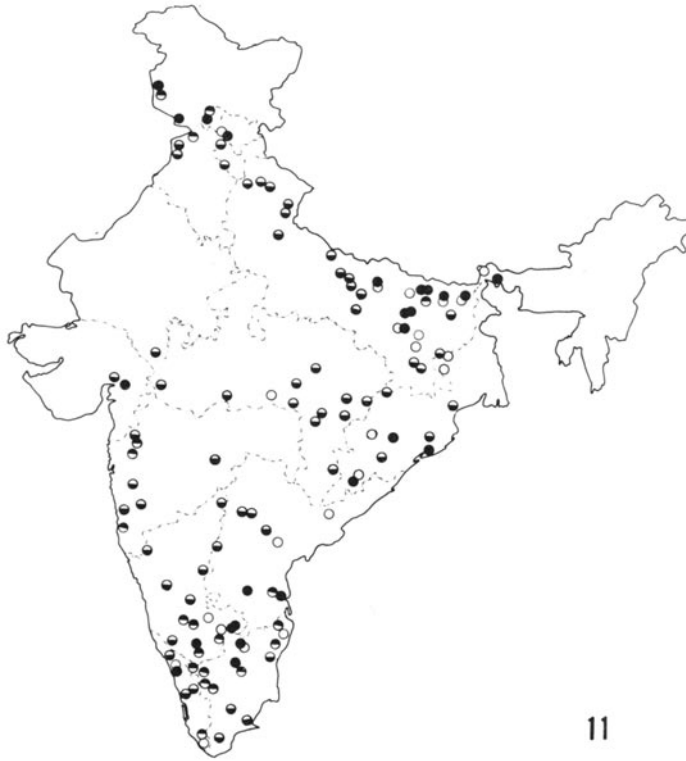


Fig. 8. Top-curved type of inflorescence of finger millet.
 Fig. 9. In-curved type of inflorescence of finger millet.
 Fig. 10. Open type of inflorescence of finger millet.



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Fig. 11. Distribution of finger millet in India. Solid circles ●: top-curved inflorescence. Open circles ○: open type of inflorescence. Upper half solid ◐: in-curved inflorescence. Lower half solid ◑: unknown type of inflorescence.

nerves and are 1.8–5 mm long. Grains are yellow to violet in color, more or less globose, 1.2–1.8 mm long, finely striated, and with a depression enclosed by a ridge marking the position of the embryo.

DOMESTICATION OF *ELEUSINE CORACANA*

Archaeological data usually provide the best evidence as to the time and place of domestication and evolution of crops. Incorrectly identified material, however, can be misleading. Two archaeological specimens have been assigned to *Eleusine*. The one is from Africa, and comes from Inyaga in Rhodesia, at about 8517 ft altitude (Summers, 1958). This undisputable material of subspecies *coracana* was dated to the 8th Century A.D. The other archaeological record is from India. Vishnu-Mittre (1968) identified carbonized seeds of both *E. coracana* and *E. indica* from Hallur (1800 B.C.) in Mysore State. These carbonized seeds were kindly made available by Vishnu-Mittre for study by this labora-

tory. We found no *E. indica* among these samples. The carbonized seeds are almost twice as large as those of *E. indica*, and lack the characteristic sculpturing of this species (See Phillips, 1972 for illustrations). Furthermore, they do not conform with laboratory carbonized grains of finger millet. Unlike finger millet grains, they are characterized by smooth surfaces and the characteristic depression that marks the position of the embryo is absent. Vishnu-Mittre (personal communication) now agrees that *Eleusine* is absent from among the carbonized plant remains obtained from Hallur.

Available evidence suggests East Africa as the area of domestication of *Eleusine*. Clark (1967) referred to the Eastern Sudan Zone as the area of finger millet domestication. Davies (1968) singled out Ethiopia, and Seddon (1968) specified the Gregory Rift area of Ethiopia as the most likely place of domestication of this cereal. Harlan (1971) proposed the highlands that stretch from Ethiopia to Uganda as the place of domesti-

cation. Shaw (1976) suggested that Late Stone Age people domesticated finger millet in East Africa whence it was transported to India by the middle of the 2nd millennium B.C. Conclusive evidence to support any one of these assumptions, however, is completely lacking.

The crop has several Sanskrit names, Rajika (De Candolle, 1967), Rajika, Raji, Rajikay (Porteres, 1951, 1958), and Raga, Ragi, Rajika (Iyengar et al., 1955-6). The basic meaning of the Sanskrit work is "red" (Apte, 1965), and only when combined with another descriptive word can these names signify a specific plant. Moreover a Sanskrit name does not necessarily indicate antiquity in India. The Sanskrit names for guar (*Cyamopsis tetragonoloba*) as an example, cannot be traced back beyond the 19th Century A.D. (Hymowitz, 1972). Porteres (1970) indicated that Arabic-African names of this crop, "tebum, telbum, talban", can be traced to the stem of the Nubian word "to cultivate". Other African names were found to mean "beer or mead". These drinks are significant items in the rituals of some of the East African tribes. Porteres (1970) concluded that linguistic evidence suggests an African rather than Indian origin for this crop. Finger millet is absent from ancient Egyptian tombs (Woenig, 1897). This, however, is not surprising. It is a summer crop, and its cultural requirements are somewhat similar to those of sorghum (see de Wet and Huckabay, 1967). In Egypt the Nile Valley used to flood in late summer and planting time was in the fall, when wheat and barley were the principal crops.

Cytogenetical and morphological data provide almost conclusive evidence for origin and evolution of finger millet from subspecies *africana*. *Eleusine indica* ($2n = 18$) and *E. africana* ($2n = 36$) differ in ploidy level. It seems unlikely that the tetraploid ($2n = 36$) crop could have been derived from a diploid wild ancestor. Moreover, little homology exists between the genomes of *E. indica* and *E. coracana*. On the other hand, *E. coracana* subsp. *coracana* and subsp. *africana* are genetically conspecific tetraploids and gene flow between them takes place in nature. This strongly

suggests that subsp. *africana* is wild *coracana*. Morphological data agree with the cytogenetical evidence. Furthermore, subspecies *africana* is still harvested as a wild cereal. Since typically African cultivars are sympatric with subsp. *africana* in the highlands of East Africa it seems probable that the crop was domesticated there. When domestication took place is a matter for speculation at present, since archaeological evidence of time of domestication is completely lacking. The westward movement of finger millet stopped in Nigeria where fonio (*Digitaria exilis*), another African millet, is grown. This barrier to westward migration may be the poor adaptation of finger millet to high rainfall and low altitudes, but is more likely due to the preference of West African tribes for eating fonio rather than any other cereal. Cultivated eleusine was probably introduced into India by traders early in the history of the crop. Hornell (1941) indicated that trading between Africa, Arabia, and India goes back to the third millennium B.C. Finger millets grown in south India are morphologically similar to those of the African lowlands. This may suggest south India as the place of entry.

SUMMARY

Eleusine coracana (L.) Gaertn. subsp. *coracana* (Finger millet or eleusine) is a cereal that is widely cultivated in Africa and India. Archaeological records of finger millet are few and unsatisfactory. But, distribution, linguistic and historical evidence seem to suggest an African rather than Indian origin of the crop. Data from morphology, supplemented with cytogenetical observations and distribution revealed that *E. coracana* subsp. *africana* is wild finger millet. This subspecies is widely distributed along the highlands of East Africa. Consequently, it is concluded that finger millet originated in the East African Highlands and was subsequently introduced into India.

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