■ **TUNISIA**

The Evolutionary History of *Pennisetum Glaucum*

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Abstract

Cereals designated as millet have played a role in subtropical and tropical regions of Asia and Africa since antiquity. Millet and sorghum are among the oldest of domesticated cereals, and in the ancient world they were common bread grains. Millet was used as food in prehistoric times. The evolutionary history of pearl millet is not yet clearly established. Several authors agree that domestication has taken place in Africa but different geographical origins for this crop have been proposed along the sahelian zone from Mauritania to Sudan. It is the only African cereal for which there exists archaeobotanical evidence. Archaeobotanical evidence from sub-Saharan West Africa suggests that pearl millet was the predominant, or even the only, cultivated cereal across the region including Mauretania, Mali, Ghana, Burkina Faso, and Cameroon during the period 2400-2200 BP. Millet spread from Africa to India where it developed easily, and even reached China, where now it has virtually disappeared. It has spread into northern Africa (Tunisia, Morocco, and Algeria) and even Spain, where it is still cultivated.

Phylogeny of Millet

The grass family (*Poaceae*) includes approximately 10000 species (Watson and Dallwitz 1992) that are classified into 600 to 700 genera (Watson and Dallwitz 1999). This family originated in the late Cretaceous according to both recent fossil data (Prasad *et al.* 2005) and molecular calibrations (Janssen and Bremer 2004). The core *Poaceae* split into two major clades: the BEP (*Bambusoid eae+Ehrartoideae+Pooideae*) and the PACCMAD (*Panicoideae+Aristidoideae+Centothecoideae+ Chloridoideae+Micrairoideae+Arundinoideae +Danthonioideae*) clades (Bouchenak-Khelladi *et al.* 2008).

Regarding the genus *Pennisetum*, the species are classified into five sections: *Pennisetum, Heterostachya, Brevivalvula, Gymnothrix,* and *Penicillaria* (Brunken 1977; Staph and Hubbard 1934). The section *Pennisetum* gathers the cultivated species from the primary and secondary gene pool: millet (*P. glaucum*, 2n=2x=14) and elephant grass *(P. purpureum*, 2n=4x=28), respectively. The chromosomal races or cytotypes *P. orientale* (2n=18, 27, 36, 45, 54) and *P. pedicelatum* (2n=36, 45, and 54) are found among the perennial species of the tertiary gene pool (Jauhar and Hanna 1998).

True millet or pearl millet from the subfamily *Panicoideae*, to which many regionally important cultivars belong (for instance, *Eragrostis tef, Eleusine coracan, Echinochloa frumentacea, Pennisetum glaucum, Setaria italica*), is distinguished from sorghum (*Sorghum bicolor*), which belongs to the subfamily *Andropogonoideae* and is cultivated worldwide. Pearl millet is a diploid, with a basic chromosome number of seven, and a haploid DNA content of 2.5 pg (Allouis *et al.* 2001). Good genetic maps, encompassing the seven linkage groups are available (Devos *et al.* 1995; Liu *et al.* 1994), and their relationship to the maps of other grass species has been established (Devos *et al.* 2000). Pearl millet has a haploid genome size of 2450 Mb (Martel *et al.* 1997)

Evolutionary History of Millet

Cereals designated as millet have played a role in subtropical and tropical regions of Asia and Africa since antiquity. Millet and sorghum are among the oldest of the cereals, and in the ancient world they were common bread grains. Pearl millet was used as food in prehistoric times, and little is known concerning its origin. Some studies believe that it was the first cultivated crop and was grown in the so-called Hoe-Age, which preceded the Plow-Age (Anderson and Martin 1949). Its use as a food in India, China and Egypt began before written records. In antiquity and in the Middle Ages, millet was grown in most of the known world. During the Middle Ages, it was one of the principal foods of the poor people in Rome and in Europe generally. During the 19th century, pearl millet was gradually superseded in Western Europe by wheat, rye, rice, maize and potatoes, which usually produce higher yields than pearl millet (Adolph and Cheng 1935).

The evolutionary history of pearl millet is not yet clearly established. The wild progenitor of pearl millet was identified as *Pennisetum glaucum* ssp. *monodii* (Brunken 1977; Harlan 1975). This species is found across the sahel zone in Africa (Brunken 1977; Harlan 1975). Archaeobotanical evidence for pearl millet in Africa is sparse, but gradually improving (Nixon *et al.* 2011). The first authors to claim an African origin for pearl millet were Koernicke and Werner (1885) and this has been generally accepted.

Some authors proposed that pearl millet is the product of multiple domestications (Harlan 1975; Porteres 1976), but others proposed a single domestication (Manning *et al.* 2011; Marchais and Tostain 1993). Several authors agree that domestication has taken place in Africa (Harlan 1975; Marchais and Tostain 1993; Porteres 1976), but different geographical origins for this crop have been proposed in the sahelian zone from Mauritania to Sudan.

Archaeobotany has placed pearl millet domestication on the margins of the Sahel more than 3000 years ago (D'Andrea *et al.* 2001; Tostain 1998). Recent proposals situate this event in the third millennium BC in the far western Sahel, perhaps in Mauritania and/or northeast Mali (Fuller *et al.* 2007). One of the emblematic sites of Central Nigeria, the Nok region, has produced a large amount of millet dated to 800-450 cal BC (Kahlheber *et al.* 2009).

One of the oldest references to the cultivation of pearl millet is that of Leo Africanus (XVI century) who reported that this crop was grown in the kingdom of Oulata in Mauritania (Brunken 1977). Vavilov (1951) has also reported the African origin of millet (Abyssinia and Sudan).

Impressions of wild millet were also found on pottery dating from about 5000 years ago in central Sudan (Stemler 1990). Burton and Powell (1968) found the greatest diversity of morphological types introduced from Central Africa and they concluded that pearl millet came from that region. The presence of chromosome schedules, characteristics of primitive types, varieties in Niger and Sudan also argue for an African origin (Pantulu 1960; Powel and Burton 1966). The origin of pearl millet is further supported by the many wild relatives encountered on the African continent, which so far are absent in India (Murty *et al.* 1967). It is the only African cereal for which existing archaeobotanical evidence, in particular grain measurements, are recovered from a series of sites in Africa and India (Fuller 2007).

One of the oldest archaeobotanical evidence of the cultivation of pearl millet has been found in Mauritania dating around 3500 BC at Dhar Tichitt (Amblard and Pernes 1989; Bhattacharjee *et al.* 2007; Munson 1976). However, proof of cultivation of pearl millet was also discovered in Ghana around 3460 BC at Birmi (D'Andrea *et al.* 2001; D'Andrea and Casey 2002), and near Lake Chad in Nigeria between 3500–3300 BC (Kahlheber *et al.* 2009; Klee *et al.* 2004).

Tostain (1998) proposed a date of

domestication around 8000 BC, and a spread of pearl millet cultivation in Asia around 4500 to 5000 BC. These data are compatible with archaeological data even though the archaeologically oldest evidence found in Mauritania date back to only 3500 BC (Amblard and Pernes 1989). In the future, archaeological remains will hopefully permit a more precise estimation of the timing of pearl millet domestication and of the spread of the cultivation of this important sahelian crop.

Archaeobotanical evidence from sub-Saharan West Africa suggests that pearl millet was the predominant, or even the only, cultivated cereal across the region including Mauritania, Mali, Ghana, Burkina Faso, and Cameroon (D'Andrea and Casey 2002; Fuller *et al.* 2007; Klee *et al.* 2004; Neumann 2005). However, the date for this evidence was never older than the early second millennium BC. Domesticated pearl millet had already spread to India in the third millennium BC (Fuller 2003; Neumann 2005). Recently, Manning *et al.* (2011) reported that the Lower Tilemsi Valley in Mali constitutes the earliest archaeobotanical evidence for domesticated pearl millet predating other finds from Africa or India by at least a few centuries.

Beyond Africa, the evidence is extremely weak for the domestication of pearl millet, plagued by misidentifications. Nonetheless, at least some of the material from India is indeed pearl millet (Fuller *et al.* 2004). Shortly after pearl millet left Africa and spread to India, it developed easily. From India, pearl millet reached China, where it has now virtually disappeared. It spread into northern Africa (Tunisia, Morocco, Libya and Algeria) and even Spain, where it is still cultivated. Zohary and Hopf (2000) claim that pearl millet was introduced into southern Spain following the Moorish invasions in the 8th century. Pearl millet cultivation in Europe dates to the 16th century (Portères 1976).

In the late 1st millennium BC, pearl millet had also been introduced to the previously winter-crop-focused farming of the Fezzan in Southern Libya (Schoenbrun 1993). Pearl millet was cultivated across most of North Africa at one time and a word for it is attested to in most Berber languages. Meillassoux (1972: 390) discusses the reference in Ibn Battuta to the trade in *anli*, pearl millet, in the 14th century in the Iwalata area, using the Berber term.

The archaeobotany of crop repertoires in the Saharan oases usually show wheat and barley in the initial phases with pearl millet appearing somewhat later. It is suggested here that the early Berbers encountered the crop as a staple in the hands of those they traded within the Central Sahara. Only later did

Figure 1: Apse mosaic in Sousse: decor "strewn" around a crown and Xenia surmounted by four millet stalks forming the emblem of one of the association's organizing theatre performances (3rd century AD).

they begin to cultivate it for themselves in the oases. The origin of the word itself is problematic, as it is not obviously similar to any sub-Saharan language. Tukulor '*nutil'* and Songhay '*hèèni'* are possible resemblances but hardly convincing (Blench 2010).

Camps (1992) noted in his study, in the Maghreb prehistory, the presence of Mediterranean plants whose pollen is found today. He signalled the presence of two fossilized pollen grains belonging to cultivated pearl millet dating from 6000 years ago (deposit at Amekni to 40km northwest of Tamanrasset in Algeria). We can therefore say without fear of contradiction that pearl millet was known in North Africa since the Neolithic, as evidenced by the numerous jars, jugs and utensils collected in the archaeological layer. The field has also revealed the presence of a large mass of sherds and vases with hemispherical bottoms, similar to those still today are used for the preparation of millet porridge. Africans have cropped pearl millet for 6500 years (Camps 1992).

It is difficult to determine when and who introduced pearl millet into Tunisia. According to Colmeiro (1885) (Brunken 1977), pearl millet was introduced into Spain from North Africa after the invasion of the Moors towards the 8th century AD. We can therefore conclude that pearl millet has been cultivated in North African countries since at least the 8th century. The semicircular mosaic found in Sousse museum (Figure 1) dating from the 3rd century AD signals the presence of pearl millet. The Roman fresco shows four pearl millet stalks around other foods, which indicates that pearl millet was already part of the eating habits of this civilization. According to Pernès (1980) autochthonous pearl millet is derived from Nigerian pearl millet.

Conclusion

The evolutionary history of pearl millet is not yet clearly established. While the archaeobotanical picture in Africa is beginning to become clearer, there are striking gaps elsewhere in the world. The obscure and probably complex origins of *Pennisetum glaucum* have made it difficult to furnish a clear interpretation of its presence in different geographical areas. Due to its strong out-crossing breeding behaviour, pearl millet likely originated from several independent domestication events and a wide range of environmental conditions. Wider context data from archaeobotany, botany, ecophysiology, climatology and genetics needs to be synthesised rather than studying data in isolation in order to construct robust models of the origins and spread of pearl millet.

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