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THE CENTRE OF ORIGIN AND DOMESTICATION OF *ENSETE VENTRICOSUM* (WELW.) CHEESMAN AND ITS PHYLOGENETIC RELATIONSHIP TO SOME *MUSA* SPECIES

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ABSTRACT: *Ensete ventricosum* is one of the species in the genus *Ensete* whose species composition is not yet known. This paper attempts to trace the origin of domesticated enset and early food production in Ethiopia, historical evidence of its distributions, botanical and genetic diversity of cultivated and wild enset forms. Based on ecological distribution of wild enset in Ethiopia, the highly dissected terrain of lower altitudes of South and Southwestern drier zones might be the initial sites of enset domestication. The complexity of enset culture and its use value and in South and Southwest of Ethiopia indicate longer period of enset cultivation. The existence of an early and dynamic root and tuber crop-based agriculture before seed and fruit-based crop system also support the early domestication of enset in South and South West of Ethiopia. A molecular genetic data from RAPD, chloroplast and ITS DNA sequence suggest that different clones of cultivated enset seem to have originated from different clones of wild enset suggesting the existence of several microcentres of domestication in the region. The wild enset forms and the cultivated forms seem to introgress and escape to the wild and domesticated sites of enset, respectively. RAPD and ITS molecular data as well as complete sequences of transcribed spacers and introns from trnT terF region of chloroplast DNA from thirteen species of *Musa* and three species of *Ensete*, including the cultivated and wild species of *Ensete ventricosum* indicated that *Ensete glaucum* and *Mussa beccarii* represent ancestral forms of *Ensete* and *Musa*, respectively. The data also showed that *E. ventricosum* cannot be reduced to *E. glaucum*, nor can *E. gilletti* be reduced to *E. ventricosum*, as some authorities have suggested. *Ensete gilletti* or a species very close to it appears to be the ancestral species of *E. ventricosum*.

Key words/phrases: Centre of origin and domestication, *Ensete ventricosum*, Molecular data, *Musa* species.

INTRODUCTION

Ensete ventricosum is an important commodity and a staple diet for a large section of Ethiopian community. The progress of research on cultivated enset in Ethiopia has been well documented (Taye Bezuneh and Asrat Feleke, 1966; Taye Bezuneh *et al*., 1967; Seifu Gebremariam, 1996; Endale Tabogie *et al*., 1996; Mulugeta Diro *et al*., 1996; Taye Bezuneh, 1996). Seifu Gebremariam (1996) listed the major problems in Enset production

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such as land fragmentation and population increase, nutritional, and production constraints due to disease, lengthy cultural practices and labour intensive processing. Mulugeta Diro *et al*. (1996) and Morpurgo *et al*. (1996) reviewed the propagation studies of the crop until 1993. These review papers, in general, covers the attempts made since the 1980's on collection, evaluation and maintenance of germplasm; clonal and environmental agronomic trials with NP fertilizers, frequency of transplants, population density, selection of suitable intercrop and observation on ecological adaptation.

The research effort so far made on enset has been limited given the importance of the crop in the Ethiopian traditional agriculture and culture. Consequently, there are several gaps to be filled and research topics to be covered with interdisciplinary approach by involving many national institutions. The research on micropropagation and diversity studies conducted by Genet Birmeta *et al*. (2004) and enset production and productivity studies of Admasu Tsegaye and Struik (2002) considerably contributed to the understanding of enset.

The other recent research progress has been on the physico-chemical properties of enset starch which can be locally produced in abundant quantities for industrial application in the manufacturing of products such as food, textile, paper, adhesives and pharmaceuticals. Tsige Gebre-Mariam and Schimidts (1996) and Tsige Gebre-Mariam *et al*. (1996) provide information on its composition, morphology, and selected physico-chemical characteristics of the starch of *Ensete ventricosum* and that proved useful when considering various applications of the starch such as in the pharmaceutics and the food industries. According to Tsige Gebre-Mariam and Nikolayev (1993), enset starch can be used both as a tablet binder and disintegrant with a better binding ability and less disintegrating power than potato starch. The disintegration time for the tablets of chloroquine phosphate, dipyrone and paracetamol made with enset starch fall within the British pharmacopoeia limits for disintegration time of unloaded tables (Tsige Gebre-Mariam and Nikolayev, 1993).

The fact that the first food (called Safna) which is a special water squeezed from the enset pseudo stem) to be ceremonially given to the newly born baby before breastfeeding in Ari community (South Omo, Ethiopia) as reported by Shigeta (1997) quoting Gebre Yntiso (1996) may also be linked to its possible medicinal value due to some active component it might possess.

In general, enset starch quality and its industrial application as well as the active chemicals it possesses for anti-tumor, anti-nematidic and anti-bacterial treatment adds value to enset use and its contribution to sustainable development and poverty alleviation of the enset to rural communities.

The very limited accounts on the origin and domestication of *Ensete ventricosum*, based on some inferences from cultural, folk systematics, historical, climatic changes, early food production and processing, and lack of archaeological evidence necessitated the need to use chloroplast, ITS and RAPD data (Endashaw Bekele and Shigeta, 2011). Study on the centre of origin of enset and its domestication is of particular significance to its utilization, improvement and understanding of enset-man interaction and the effect of these on both natural and man-made ecosystem and the impact they make on the origin, evolution and diffusion of culture which are the very bases of adaptation and survival of the indigenous communities of enset culture.

The Genera *Ensete* and *Musa*

The genera *Ensete* Horan and *Musa* L. are grouped in the order *Zingiberales*, family Musaceae. *Zingiberales* is phylogenetically embedded within the derived eumonocots (*Arecales, Commelinales, Poales*). The order includes many conspicuous taxa, including banana (*Musaceae)*, bird of paradise (*Stretitziaceae*), heliconia (*Heliconiaceae*), and ginger (*Zingiberaceae*) (Kress *et al*., 2002). The *Musaceae, Stretitziaceae, Lowiaceae,* and *Heliconiaceae* constitute a basal paraphyletic group. This is a non-monophyly grouping that is based on shared primitive or original state characteristics (plesiomorphies) and hence typically excludes one or more taxa with unique derived characters (autapomorphies).

These families are ancestral to the sister groups *Zingiberaceae+Costaceae* and *Cannaceae+Marantaceae*, which together form a monophyletic terminal lineage (Manchester and Kress, 1993) with groupings that are based on shared primitive characters and exclude autoapomorphic taxa with unique derived character states. *Musaceae* represents the most basal lineage in the order, based on a tree derived from maximum parsimony analysis of morphological characters (Kress, 1990).

The three extant genera of *Musaceae* are *Musa* L., which was originally restricted to Asia (n = 7, 9, 10, 11); *Ensete* Bruce ex Horan, which is distributed in Africa, America, and Asia (n = 9); and *Musella* (Fr.) C.Y. Wu ex H.W.L., which is a monotypic genus endemic to Southern China (n = 9).

Although another species, *Musella splendid*, from Vietnam has been reported (see Valmayor and Phillip, 2002), many authorities consider this to be *Musella lasiocarpa*.

Cultivated bananas are sterile seed diploid, triploid, or tetraploid clones with various combinations of the A and B genomes from two diploid species of *Musa*, namely, *M. acuminata* L.A. Colla (AA genome) and *M. balbisiana* L.A. Colla (BB genome) (Simmonds and Shepherd, 1955). These wild relatives of edible bananas originated in Southeast Asia (Simmonds, 1962; 1966). As edible bananas are seedless, the presence of vegetatively propagated plants in most tropical regions is necessarily the result of human activities and somatic mutations. *Musa acuminata* and *M. balbisiana* have played a major role in the complex domestication process of *Musa* (Simmonds, 1962; Simmonds and Shepherd, 1955). Parthenocarpic, vegetatively propagating cultivars of the genus *Musa* have diversified mainly because of the accumulation of spontaneous mutations.

The genus *Ensete* is one of the smallest genus in the plant kingdom and belongs to the Family *Musaceae*, order *Zingiberales* (Tomilson, 1969). The relationship between the *Ensete* and *Musa* genomes has yet to be elucidated. Information on the relationship of *E. ventricosum*, a domesticated species, to other ancestral *Ensete* species and *Musa* is very limited. There are taxonomic problems in both genera, and some characters, such as the existence of natural suckers in *Musa* and their absence in *Ensete*, which are used to distinguish between the two genera, are not consistent, as there are some suckering clones of *E. ventricosum* (known as *Entada* and cultivated by Ari ethnic groups in Ethiopia (Shigeta, 1990) and limited and rare suckering enset clones (personal observation).

Methods used for tracing the origin of *Ensete*

Tracing the origin of enset and early food production in Ethiopia, the following sources of information were used (Endashaw Bekele, submitted for publication)

1. Historical evidence
2. Evidence from botanical, genetic and cultural sources
3. Evidences from food production and processing
4. Evidences from historical distribution of *Ensete*
5. Brandt Climatic periods based evidences

6. Murdock's suggestion, enset and livestock interaction and climatic change based evidence

7. Linguistic evidence

8. Evidences from botanical differences and diversity between wild and cultivated enset forms

9. Evidences from ecological association with root and tuber crops

10. Evidences from diverse forms of food preparation from enset

11. Evidence from ecologically isolated and dissected mountain terrains

12. Evidences from diverse use value of enset

13. Evidences from molecular genetic diversity and systematics of *Ensete* and *Musa*

DISCUSSION ON THE CURRENT STATUS OF ENSET, GAPS AND CHALLENGES

I. Taxonomic problems and species distributions in *Ensete*

The taxonomy of the genus *Ensete* has not been fully resolved and remains a subject of debate, although the genus is among the smallest in the plant kingdom. *Ensete ventricosum* is a staple cultigen for much of the Ethiopian community, and its use is still expanding. In 1882, Horaninow, quoted in Baker and Simmonds (1953), was the first to propose *Ensete* as a new genus. Cheesman (1947) recognized 25 species, whereas Baker and Simmonds (1953) identified only about 8 distinct species, and Simmonds (1960) listed just 6 species, with 1 or 2 undescribed species in Thailand.

The currently recognized species are *E. gilleti*, *E. glaucum*, *E. homblei*, *E. perrieri*, *E. superbum*, *E. ventricosum*, and *E. wilsonii*. Simmonds considered *E. wilsonii* to be *E. glaucum* and also, noting the absence of consistent differences between *E. ventricosum* and *E. glaucum*, it can be suggested that the former be reduced to the latter. It was also recommended that *E. gilleti* be reduced to a subspecies of *E. ventricosum*. Both Cheesman (1947) and Simmonds (1960) noted that *M. martini* Noter from Vietnam might belong to *Ensete*.

E. gilleti De Wild is native to western Africa, and distributed from Sierra Leone to Angola, and is ecologically adapted to drier locations than other *Ensete* species. *E. homblei* Beq. ex De Wild is more like the canna and banana distributed in Congo and Zambia. *Ensete perrieri* is reported from Madagascar, and *E. superbum* Roxb is native to India. *Ensete glaucum* Roxb is distributed over a wide area from Burma to the Philippines and Java (Indonesia).

Ensete ventricosum

Two *Ensete* species might also occur in North America (Simmonds, 1960; 1962; Manchester and Kress, 1993). In Africa, *E. ventricosum* is the most widely distributed and highly variable species. It widely occupies the whole of central Africa, from Cameroon to Ethiopia and South Africa. Although generally adapted to swampy and moist areas throughout central and eastern Africa, it is cultivated only in Ethiopia, for food and fiber. In Ethiopia, the wild form of *E. ventricosum* is found at lower altitudes, in a relatively drier zone than the distribution of the cultivated form.

Analysis of genetic diversity among cultivated enset (*Ensete ventricosum*) populations from Essera and Kefficho, South western part of Ethiopia using inter simple sequence repeats (ISSRs) marker resulted in clear demarcation of cultivated enset clones from various regions (Dagmawit Chombe and Endashaw Bekele, 2011). Endashaw Bekele and Shigeta (2011) have analyzed complete sequences of transcribed spacers and introns from the trnT-trnF region of chloroplast DNA (cpDNA) from Musaceae species to establish the phylogenetic relationships among 3 species of *Ensete* and 13 species of *Musa*.

Parsimony analysis and pair-wise distance data produced a single tree, with *Ensete* and *Musa* as clearly distinguished clades. Six *Musa* and three *Ensete* clades were generated. The topology of these clades did not change when the data were split into spacers and introns, although the split resulted in poor bootstrap support. Removing a hotspot from the entire dataset improved clade support. The clades produced were discussed with reference to existing taxonomic treatments.

In contrast to previous suggestions, most of the *Rhodochlamys* species that were investigated clustered together with strong support establishing their distinctiveness from the *Musa* species, s. *Ensete glaucum* and *M. beccarrii* appear to represent ancestral forms of *Ensete* and *Musa*, respectively, and both have a common ancestor that is yet to be established. Our data also showed that *E. ventricosum* cannot be reduced to *E. glaucum*, nor can *E. gilletti* be reduced to *E. ventricosum*, as some authorities have suggested. *Ensete gilletti* or a species very close to it appears to be the ancestral species of *E. ventricosum*.

ORIGIN OF ENSET

The following are major summaries and points accounting the centre of origin for *Ensete ventricosum*.

- Agronomists and biogeographers have long considered the Ethiopia primary origin for enset agriculture.
- Anthropologists, archeologists, and historians and other scholars argue for the domestication of enset in Ethiopia as early as 10,000 years ago.
- Stiehler (1948) believed that the indigenous hunter/gatherer of southern Ethiopia were first to cultivate enset.
- Some historians and botanists had earlier attempted to trace the origin of enset to ancient Egypt.
- Writers, such as Smeds, 1955 suggested that enset cultivation originated in highland Ethiopia.
- Smeds (1955) speculated that the present Wolaita-Kambata-Gurage regions, is the original centre of enset cultivation.
- Murdock (1959) suggested sometime in prehistory “Sidamo tribe” of the southwestern Ethiopia independently brought enset under cultivation.
- Ehret (1979) proposed theory based on largely upon historical and linguistic data that argue for much earlier date for the beginning enset food production (10,000 years ago).
- Brandt (1996) proposed a model for the evolution of enset food production in Ethiopia by considering the following climatic periods: Terminal Pleistocene hyper aridity (ca 18-10,000 B.P) with initial domestication of enset and other plant foods; Early-middle Holocene climatic optimum (ca 10-5000 B.P) with population increase and colonization of new lands and beginning of deforestation; Middle-later Holocene (ca 5-2000 B.P) with the development of more complex social, economic and technological system: methods of postponing consumption and spoilage of crops i.e., fermentation and storage of enset in above and below-ground devices; Latest Holocene (.D. 500-1900) with the development of Ethiopian feudalism; increasing pressure on peasants to grow surplus/cash crops and eventual abandonment of enset and other

subsistence crops in North and Northwest.

The genetic diversity parameters of the enset populations of SW Ethiopia studied is indeed high. The results based on ISSR is in agreement with other result obtained by AFLP (Almaz Negash *et al*., 2002), RAPD (Genet Birmeta *et al*., 2002) that indicated that the diversity and number of clones in enset cultivation regions could be as high as the number of vernacular naming used by local farmers.

The higher within genetic diversity in cultivated enset observed by various studies could be due to:

- The vegetative propagation mode of reproduction;
- Other factor such as protection of enset clones due to cultural reasons;
- The differential values obtained from each clones of the crop; and
- Shannon diversity index and GD result showed that populations of enset from some sites are more diverse than populations from other areas.

A clear separation with minor admixture between the enset clones from various regions have been noted with relatively high to medium level of gene flow detected and this may be due to exchange of materials between peoples of the various regions, therefore, gene flow will not be restricted between clones from the various regions.

Morphological, cultural, use value and molecular diversity strongly suggest that Ari, Dawuro, Bonga and Sidama each with one site representation be selected as sites for *in situ* field conservation sites for *E. ventricosum*.

RAPD and ITS data that were gathered demarcated the eight *Musa* species and cultivated and wild forms of *Ensete ventricosum* suggesting that different clones of cultivated enset seem to have originated from different clones of wild *Ensete ventricosum*. This suggests that several microcentres of domestication exist in the region. The wild and cultivated forms of *Ensete ventricosum* introgress to each other.

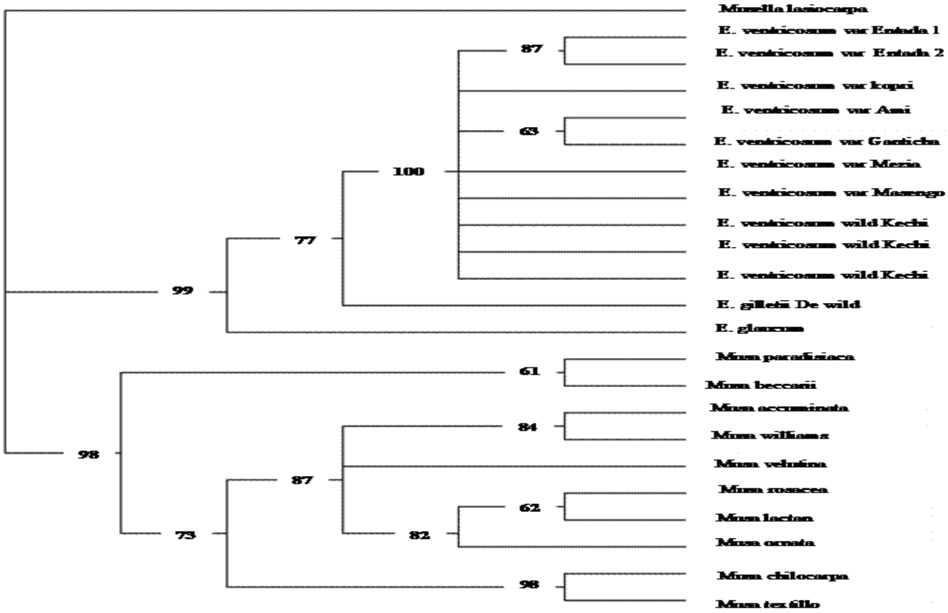
The chloroplast DNA sequence data gathered from three species of *Ensete* and 13 species of *Musa* resulted in the following conclusions:

- Three species of *Ensete* and thirteen species of *Musa*. Parsimony analysis and pair-wise distance data produced a single tree, with

Ensete and *Musa* as clearly distinguished clades. Six *Musa* and three *Ensete* clades were generated. The topology of these clades did not change when the data were split into spacers and introns, although the split resulted in poor bootstrap support.

- In contrast to previous suggestions, most of the *Rhodochlamys* species that we investigated clustered together with strong support establishing their distinctiveness from the *Musa* species studied. *Ensete glaucum* and *M. beccarrii* appear to represent ancestral forms of *Ensete* and *Musa*, respectively, and both have a common ancestor that is yet to be established.
- The data also show that *E. ventricosum* cannot be reduced to *E. glaucum*, nor can *E. gilletti* be reduced to *E. ventricosum*, as some authorities have suggested. *Ensete gilletti* or a species very close to it appears to be the ancestral species of *E. ventricosum*.

As shown below the three species of *Ensete* and 13 species of *Musa* Parsimony analysis and pair-wise distance data produced a single tree, with *Ensete* and *Musa* as clearly distinguished clades.



Strict consensus tree of hundred equally parsimonious trees generated (length = 223 steps, CI = 0.88, RI = 0.90, RC = 0.79, more see table—) from the combined dataset of trnT-F (AB+CF) region using substation only. Bootstrap values greater than 50% are indicted above the branches.

Fig. 1. Strict consensus tree of 3 species of *Ensete* and 13 species of *Musa* derived using parsimony analysis and pair-distance data.

SYNTHESIS, KEY MESSAGES AND CONCLUSIONS

The species composition of the genus *Ensete* is unsettled and need further treatments. The distributions of the various currently recognized species of the genus in Africa and Asia and a systematics account of its origin and domestication still has a gap. One of the reasons for the disputes on the centre of origin in literature is partly due to unclear demarcation between the concepts of centre of origin and centre of initial domestication of a given species.

A molecular genetic data from RAPD, chloroplast and ITS DNA sequence suggest that different clones of cultivated enset seem to have originated from different clones of wild enset suggesting the existence of several microcentres of domestication in the region. These microcentres need to be further elaborated for *in situ* conservation site identification and implementation.

While archaeological evidence is completely lacking, the inferred evidences on the origin and domestication of enset need critical treatments. The research effort on enset has moved very slowly and as a result there are still several gaps to be filled and research topics to be covered with a need for involvement of many institutions.

The relationship between the *Ensete* and *Musa* genomes has yet to be elucidated. Information on the relationship of *E. ventricosum*, a domesticated species, to other ancestral *Ensete* species and *Musa* is very limited. There are taxonomic problems in both genera, and some characters, such as the existence of natural suckers in *Musa* and their absence in *Ensete*, which are used to distinguish between the two genera, are not consistent, as there are some suckering clones of *E. ventricosum* (known as *Entada* and cultivated by Ari ethnic groups in Ethiopia (Shigeta, 1990) and limited and rare suckering enset clones (personal observation).

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