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Archaeology of African Agro-systems: A Macro-Evolutionary Perspective

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Abstract: The neolithization processes – the shift from hunting-gathering to food production– was kicked off at the end of the Late Glacial Maximum and amplified at different pace in different places during the Holocene. The virtual simultaneity of these transformations in different parts of the world begs for explanation. The Early Holocene Global warming triggered profound environmental changes that offered new resources cohorts and subsistence opportunities to post-Pleistocene hunters-gatherers. Plants and animals' domestication resulting from the long-term exploitation and manipulation of selected range of species took place in different parts of the world. Different hypotheses have been formulated to understand the forces driving this shift and the mechanisms sustaining these processes. The prime-movers in these reviewed models include climate change, population growth, the dynamic of exchange, feasting, or religions. This paper focuses on the genesis of African agro-systems in a macro-evolutionary perspective. Plant domestication and the ensuing agricultural system derived from the operation of co-evolutionary process involving nature, biological entities, and human agency in constant directional feed-back loops. The derived African agro-systems, their genesis, diversity, chronology, and long-term evolution are outlined and discussed. The domestication of Pearl-millet (*Pennisetum glaucum*) as well as its expansion in the continent are featured in a case-study showcasing the core Extended Evolutionary Synthesis (EES) assumptions that are: directionality, causality, targets of selection, mode of inheritance, and pace of evolution operating at micro as well as macro levels.

Keywords: Neolithization, Agriculture, Agro-systems, Agro-forestry, Macro-evolutionary, African Cerealiculture, Horticulture

1. Introduction

My research has been focused on the comparative neolithization processes around the world during the last two decades. The introductory and theoretical part of this paper are made of a synthesis of different papers published during that period [1-5]. The adoption of food production strategies – Neolithization Processes -, kicked off at the end of the Pleistocene is a crucial step in the evolution of human societies. Livestock husbandry and agriculture, the very foundation of contemporary societies, emerged at different times and places, in different environmental and cultural contexts. Starting with V. G. Childe [6] coherent explanation of the "Neolithic Revolution", generations of researchers have investigated the causes and consequences of the adoption of food-production. Different variables, ranging from climate change to population growth, including the dynamics of exchange as well as the emergence of religions, were relied upon to craft explanatory theories of the neolithization processes. None of these partial explanatory theories is satisfactory. All the variables involved played a role in the process with different emphasis depending on time, place, and culture. The adoption and generalization of food-production strategies are the product of macro-evolutionary processes linking many non-linear dynamic systems. They include the complex web of relationship between climate, soils, vegetation, fauna, and human societies. Thanks to the impressive developments of genetics and genomics, plants and animals' domestication processes can be probed and integrated within a macro-evolutionary framework. "Domestication is a complex process along a continuum of human, plant, and animal relationships that often took place over a long time period and was driven by a mix of ecological, biological, and human cultural factors" [7].

2. Research Goals: Review of Initial Theories and Models

The neolithization processes, manifest through the domestication of plants and animals and their co-related socio-political and ideological transformations, resulted in the shift from hunting and gathering to progressive and increasing reliance on food-production. In all the cases, they operated in three successive stages: 1) - resources management and selection; 2) - domestication of selected species; and 3) - development of agricultural and livestock husbandry systems. Increasing number of syntheses of archaeological and population genetic data show that the initial steps of domestication were not a rapid evolution of cultivated plants but instead a protracted process [8].

Attempts at a general theory of the neolithization processes, initially based on the "prime-mover" rationale, can be arranged into three successive and partially overlapping generations. Gordon Childe [9] was the first to craft a comprehensive theory of the shift from hunting-gathering to food-production. It was dubbed "the Neolithic Revolution", in analogy to the "Industrial Revolution". Much has been written about the "Childean" use of the concept of revolution in this regard. But Gordon Childe was clearly referring to the profound economic, social, and political consequences of this change in subsistence systems. A change that laid the foundations of "modern" settled village life and later the "Urban Revolution".

The "Oasis" or "propinquity theory" posited climate change as the prime-mover for the dramatic shift from hunting-gathering to food production at the end of the Pleistocene. According to the drafted scenario, the global post-pleistocene warming of the earth climate resulted in the extension of arid lands and deserts. Plants, animals, and humans were confined to a few restricted and favorable oasis-like areas, along the major rivers of the Fertile Crescent, the Tigris, Euphrates, and in a certain sense the Nile – Yellow River and Yang-Tse River in China -. Humans took advantage of the situation to initiate the cultivation of some of their favorite plant food – wheat, barley, emmer, lentils --. And in the process allowed the wild mammals herds to feed on their fields after harvests, and from there, initiated livestock husbandry. These initial stages in the practice of agriculture and livestock husbandry led to sedentary village-life and the invention of pottery [10-11]. Childean theory was un-rivaled for several decades up to the late 1950's early 1960's.

The first systematic objections to G. Childe, "Neolithic Revolution" narrative were raised by Robert Braidwood [12]. He questioned Childe's suggestion of a general onset of aridity all over the Near-eastern Fertile crescent and launched the first coherent multi-disciplinary field research project at Jarmo, in the Zagros mountains in Turkey. The research team from the University of Chicago Oriental Institute included soils scientists, fauna and plants analysts, as well as experts in different domains of material culture archaeology. The starting point of Braidwood reasoning was anchored on the environmental diversity of the Fertile Crescent. It is made of coastal plains along the Mediterranean Sea, hills, plateaus, mountain ranges, hilly flanks and valleys. This diversity had significant implications for the natural distribution of wild plants and animals, and their pattern of change through time. The record from the Early Neolithic site of Jarmo did not show any evidence of a sustained shift toward increasing aridity at the end of Pleistocene. Small mammals like goats were hunted and later domesticated in that area. A comparative analysis of the material from other sites points to significant regional variation in the shift toward food-production. For Braidwood, this suggested that each area had its own specific evolutionary trajectory, derived from its peculiarities. He drew on the plant geneticist N. Vavilov concept of "Nuclear zone", and dubbed his hypothesis the "Nuclear zone theory". In contrast to Childe, Braidwood did not address the "why" question. Instead, he explained the shift to food-producing economies as a timely change in the long-term socio-cultural evolution of human societies and cultures.

These two approaches to the neolithization processes featured environmental change and its impact on human subsistence and social systems on the one hand (G. Childe), and human – or better cultural - agency in the other (R. Braidwood). These major dimensions, with different dosage, are components of each of the theories that came to be crafted later, in the second and third generations.

The second generation of explanatory theories is characterized by more elaborate scenarios combining environmental change and population dynamics. There are interesting nuances between authors. Cohen "food crisis" hypothesis [13] and Binford [14] "marginal zone theory" provide a good sample. For Cohen, relying on the number and elaboration of Levantine Epi-Paleolithic – or Mesolithic elsewhere – sites, there was a sustained population growth during the late Pleistocene as shown by the number of Natufian sites. This dynamic demography threatened the subsistence sustainability of Epi-paleolithic hunting-gathering societies. They consequently, adjusted to the new situation through selective and intensive exploitation of a narrow range of plants and animals species, triggering their domestication.

Binford's marginal zone theory is also anchored on population growth with however a more systematic integration of the spatial – or better territorial – dimensions. Accordingly, Late Pleistocene hunter-gatherers intensification – as indicated by the Natufian case for example – took place in the cores of different "nuclear zones" with the development of bulkier dwelling features, storage facilities, as well as systematic burials within and between habitation units. According to Binford's model, this sustained population growth triggered out-migration from the cores areas to the marginal periphery, along moving-frontiers. It is in these contexts that the new settlers carrying their cultural baggage proceeded to preserve their original food-ways and initiated what later became the domestication of a range selected plants and animal species. In other words, the neolithization process that resulted in the emergence of agriculture and livestock husbandry took place along the margins of the core-areas instead of their centers.

The third generation theorists were critical of what they saw as "environmental deterministic" approaches to the neolithization processes. They pointed to the neglect of socio-cultural mechanisms that may have been part of the process and suggested alternative with more explicit and systematic integration of socio-cultural practices with long-term consequences.

B. Bender [15] formulated the "exchange theory", anchored on environmental complementarity, social dynamics, and mobility patterns of foraging groups. The impetus for this model came from the discovery of intriguing archaeological finds - like sea-shells from the Mediterranean found several hundred or even thousand kilometers in the hinterland, in Northern Germany for example – that remained unexplained and were left floating. B. Bender suggested that they may have been part of down-the-line exchange systems linking connected late Pleistocene circum-Mediterranean foraging groups. According to Bender theory, the intensification and "routinization" of these social links led to the selection of a narrow range of resources to fuel the round of exchanges. Coastal groups may have selected a certain range of goods including peculiar and colorful sea-shells, while the hinterland groups may have brought cereals, fruits, and/or baby mammals. Seasonal gatherings of these foraging groups in their overlapping territorial ranges were a crucial mechanism of their biological and social reproduction. It is in such context that the enacted cycles of exchanges triggered sustained intensification that resulted in the domestication of a few targeted plants and animals' species. The neolithization process was therefore the consequence of the linkage loops outlined above.

B. Hayden [16] provide a more focused variant of the exchange theories aims with his "feasting hypothesis". He intended to explain the puzzling early domestication of pepper, tomatoes, and guinea-pigs in South America. These domesticates were clearly not a response to food-crises. For Hayden, large social gatherings were part of the social organization of some Late Pleistocene/Early Holocene foragers. Whatever the gatherings purpose, the assembled people had to be given food and beverages. In competitive feasting contexts, special food items were distinctive enough to set one group apart relative to the others. The feasting theory accounts for the selection of special plants and animals that may have been important elements of feasting in which elaborate items of material culture were used and displayed. The domestication of some plants and animal species was consequently an unintended consequence of the generalization of large social gatherings and feasts.

3. The Neolithic Revolution as a Revolution of Symbols

J. Cauvin [17] crafted a radical approach to the neolithization processes. In his book "*The Birth of the Gods and the Origins of Agriculture*" he distances himself from all materialist explanation of the emergence of sedentary village life, the practice of agriculture and livestock husbandry that took place in the Middle East from 10 000 to 7000 BCE. Relying on the "*Mentalités*" rationale, he argued that the onset of Neolithic life-ways was derived, not from population growth, climate change and/or forced adaptation of human communities at the end of the Pleistocene, but from a "revolution of symbols", the invention of new religions and deities, that generated new cultural practices and worldviews. He relied on a series of zoomorphic and anthropomorphic figurines and statues from different middle-eastern Late Pleistocene - Early Holocene sites interpreted as staging the new religious beliefs. The Mother-Goddess, seating on a leopard throne in Çatal Höyuk Early Neolithic sanctuary is claimed to document a radical shift in human symbolic behavior. The presence of a number of female figurines, interpreted as emphasizing fertility, is relied upon as additional supporting evidence. According to J. Cauvin rendering of the developmental sequence, a new religion articulated on Mother-Goddess and Bulls characters took shape in the Western flank of the Fertile Crescent during the Pre-Pottery Neolithic A (PPNA) and led to the adoption of Neolithic life-ways.

For Cauvin [13], the first evidence of the new revolution of symbols can be traced back to the post-Natufian El-Khiam period, around 10 000-9500 BCE, prior to the development of the Pre-Pottery Neolithic A (PPNA). Natufian art repertoire included representations of gazelles, deers, birds, and dogs as shown by finds from Wadi Hammeh and Nahal Oren. That from El-Khiam period consists essentially of female figurines, pointing to a radical shift from zoomorphic to anthropomorphic representations. The selection of the woman body icon is claimed to emphasize fertility. A conception that led to a later emergence of a Goddess-Mother figure. Such figurines were already known and widespread during the Upper Palaeolithic period but for Cauvin they were part of an above all zoomorphic and relatively anarchic system of representation because «most of these animal representations are clustered, without any evidence (…) of a dominant animal that can be considered as a supreme being figure» [18].

The new religious symbols, especially the carved or painted representations of the Goddess, spread widely in the Near-East from the end of the El-Khiam period to 7000 BCE. The Early Neolithic site of Çatal Hüyük in Anatolia is considered to have provided the most extensive evidence of this new worldview. The representation of the mother-goddess figure is associated with that of a bull. They are found in different places, frescoes, and sanctuaries, and also as smaller lightly fired portable clay figurines. Accordingly, and beside its frequent representation, it is the specific place in which the figure of the Mother-Goddess is set at Çatal Hüyük that points to its divine character. According to Cauvin, she is «dominant on the northern and western wall of the domestic sanctuaries», represented in the process of giving birth to bulls. The numerous female figurines from Tell Mureybet, Hacilar, and Çatal Hüyük point to an over-emphasis on fecundity through the exaggeration of waist and breast proportions. The control and domination over leopards are added to motherhood and fecundity symbols. For Cauvin, this symbolic system persisted during the whole Neolithic period and Bronze Age up to the emergence of Jewish monotheism.

Despite local variations, the duo «Mother-Goddess/Bull» that emphasized complementarity, but subordination of the latter to the former, points to the secularization of a new «worldview» conveying new relationship between humans and nature. How was the genesis of this new worldview connected to the shift from hunting-gathering to food-production and village life remained unfortunately un-addressed.

I. Hodder [19] presents a different view on the art from Çatal Hüyük. «It can be argued that the 9000-year-old art at Çatal Hüyük is closer to science than it is to some contemporary art, in the sense that it aims to intervene in the world, to understand how it works, to change it». This position points to a more dialectic relationship between mind and matter, society and nature. A. Testart [20] pointed to weaknesses in the reasoning crafted in Cauvin's «*Révolution des Symboles, Naissance des Divinités*» and carried out a convincing refutation of the religious assumptions imbedded in that model. The Revolution of symbols thesis ignores all environmental circumstances that are strong constraining forces on human social systems. Cauvin failure to link human's behaviors to processes operating independently in the biosphere is a serious weakness [21-24]. Paradoxically, A. Testart vigorous refutation of Cauvin's thesis is significantly weakened by his own unwillingness to take seriously into account the biological component of the domestication process.

The emergence of food-producing economies and settled life-ways are the result of contingent interaction between independent variables with mutually re-enforcing consequences. Depending on circumstances, some of these interaction loops became co-evolutionary nodes, shifting the system into a 'directed variation' mode.

4. Methodology: The Macro-Evolutionary Perspective

The Neolithization processes debate is much more subtle and fine-grained today. The "explanatory lineages" outlined above are still alive and well [25-27]. Naturalist-oriented researchers tend to consider the shift to food-production as series of adaptive adjustments to a wide array of dynamic processes. There are nuances between parallel approaches, essentially Human Behavioral Ecology (HBE) through Broad Spectrum Revolution (BSR) rationale, Optimal Foraging Strategies (OFS) and Diet-Breadth Model (DBM) [28, 29] and macro-evolutionary perspectives [30, 31]. From such integrative perspectives, the adoption of agriculture and sedentary life-ways as well as livestock husbandry and pastoral nomadism are the results of co-evolving dynamic systems. The driving forces that triggered these contextual adaptive shifts can accordingly be pinned down, analyzed, and "falsified" [32]. Domestication is clearly the core of the neolithization processes. The key variables involved include the landscape, wildlife, climate, and humans, or more precisely the complex interaction loops between these variables.

"Domestication is a process of unquestionable evolutionary impact affecting the evolutionary trajectories of humans (both biologically and culturally), the plants and animal species brought under domestication and a wide range of other organisms affected by the spread of domesticates and the agricultural economies based on their production [33].

There are different nested levels involved in the «construction of food-ways», all resulting from conscious or unconscious selection processes. The landscape, constantly impacted by humans offers a more or less wide assortments of resources, restricted in this case to plants and animals. All edible items are not eaten, and the construction of standard cultural food –staple-food – is in constant adjustment depending on circumstances. This core-category of people diets includes most of the desirable food items that are generally in large and reliable supply. Without going into the details of past «cuisine» traditions and in different parts of the world, the staple diets are made of key source of carbohydrates (wheat, barley, maize, millet, sorghum, rice, yams, bananas, manioc, etc.), plants and animal proteins (beans, lentils, cowpeas, soja, meat, fish, mollusks), and plants and animal fat (palm-oil, olive-oil, peanut-oil, animal fat, etc). Staple food is generally supplemented by occasional food. This category consists of edible items that can be relied upon as substitute or addition to the basic cultural foods. And the third and last category is that of emergency food. It is made of all edible items that can be relied on in food crises circumstances.

The acquaintance with all these food-categories is learned and transmitted from one generation to the next. There is consequently a certain inertia in the composition of staple diets that is nonetheless exposed to abrupt changes – punctuated equilibrium --. Cognition is thus crucial in modeling the shift from hunting-gathering to food-production [30-31]. Food-ways have to be regarded as cultural constructs embodying thought, communicating information, and eliciting action. They involve human minds, motor skills, and techniques.

The bursts of completely novel patterns of behavior were in all the cases followed by periods of stasis. It is axiomatic that cultural evolution is epigenetic. Once established the new behavioral patterns are learned and transmitted through habituation processes. This is generally done through «parental care», learning, transmission from generation to generation, as well as enforcement of the psycho-behavioral schemes. "The potential for directed change in cultural systems is greatly, perhaps even exponentially, enhanced over that found in biological systems by the human ability to evaluate outcomes of behavior and to abandon, adjust, or perpetuate behaviors based on this evaluation." [33, 34].

The Neolithization processes took place at different times and places within different environmental circumstances all over the world. In the co-evolutionary approach adopted in this paper, human agency is a crucial element of cultural adaptation. "It allows cultures to respond to pressures more quickly and with greater degree of flexibility and directness.". In order to explain culture change, one has to un-wrap the processes shaping different levels of the culture under investigation. Human societies are part of an inclusive trophic chain. They are inserted in a population ecology made of constantly interacting multi-components systems. The dynamics of food-complexes is driven by populational and cultural selection pressures. The operations of all these complex adaptive systems preside over the construction of cultural landscapes, in a dialectic between the "naturalization of the societies and the socialization of nature [35-36]. Domestication research is situated at the interface of biology and culture, and the emerging Extended Evolutionary Synthesis (EES) provides tools for robust analyses of the neolithization processes [37-43]. From the EES perspective, "developing organisms play a far more active constructive role in both their own development and their evolution than has been traditionally conceived". As suggested by Zeder "the domestication of plants and animals provides an ideal model system assessing core EES assumptions about directionality, causality, targets of selection, mode of inheritance, and pace of evolution.

1) – Directionality provided by variation derived from genetic and constructive developmental processes manifest itself in phenotypic plasticity. 2) – Causality operates as a reciprocal process. Organisms are not only shaped by selective environment but also shape it. In the niche construction process, acquired characteristics and phenotypic changes do not invariably follow genetic changes but may lead it. 3) - Targets of selection vary considerably. They can be genomes, genes, cells, tissues, organisms, regulatory processes, and groups of organisms. 4) - Inheritance is the transmission from one generation to the next. There are multiple systems that shape trans-generational inheritance, both internal and external to the organism. Acquired traits can be inherited with transgenerational epigenetic inheritance. And finally, 5) - the Tempo and pace of evolutionary change are very variable depending on organisms and systems. In all the cases however, evolution proceeds at an uneven pace with periods of stasis punctuated by periods of rapid macro-evolutionary change.

5. Mapping the World's Neolithization Areas

The shift toward food production took place during the Holocene period, at different times and places [44-48]. The earliest stage took place at the very end of the Pleistocene-Early Holocene and the second one in the Middle of the Holocene.

The earliest manifestations are dated to 10,000 BP in the Fertile Crescent in Western Asia. Wheat, barley, lentil, pea, chickpea, broad bean, flax and olive were domesticated between 11000 and 6000 BP as well as Sheep, goats, cattle, and pigs (figure 1). With variation from one area to the next, the western Asia complex consisted of mixed economies, combining cereal agriculture and livestock husbandry. This complex spread later around the Mediterranean and continental Europe.

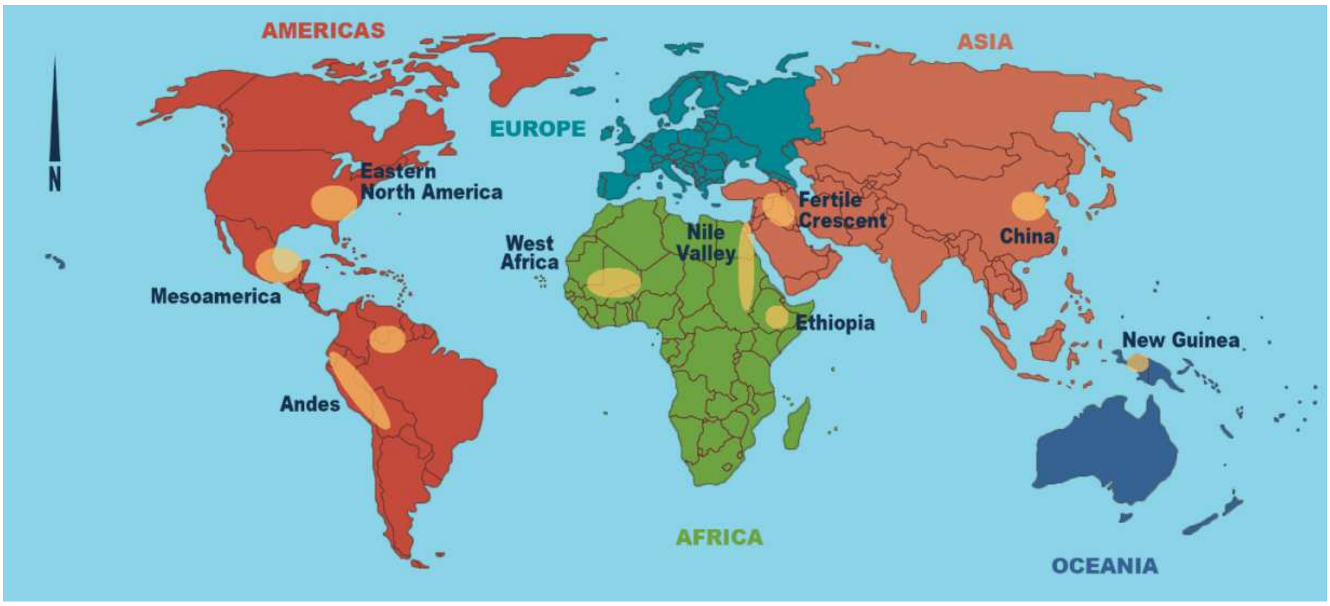

Figure 1. *World's neolithization areas.*

In Eastern Asia, foxtail millet, rice, and pigs were domesticated around 8000 BP. Broomcorn millet, foxtail millet and pigs remains were found in the Yellow river basin in northern China. Rice, foxnut and pigs remains are document in the Yangtse river basin in central/southern China (figure 2). Silkworm, yak, horse, Bactrian camel, duck and chicken were domesticated later during the Middle Holocene, between 5500 and 4000 BP. Both complexes spread all over Eastern Asia, reaching the Korean Peninsula, Japan, southwestern China and the Himalaya. The timing and selected species were different in south Asia. Zebu cattle and water buffalo were domesticated between 8000 and 4500 BP, followed by tree cotton, rice (*O. indica*), little millet, brown top millet, mung bean and pigeon pea from 4500 to 3500 BP.

The Kuk swamp in New Guinea provides evidence for the intensive exploitation and domestication of bananas, plantain, and yams (*Dioscorea alata*) between 7000 and 4000 BP (figure 2). This complex spread later throughout the Indian Ocean to reach Africa.

Squash, sunflower, sump-weed, and pit-seed goosefoot were domesticated in North America between 5000 and 4000 BP. Further South, in Meso-America, plants and animal domestication operated in three distinct phases. Squash (pepo) and maize were domesticated at the beginning of the Early Holocene, between 10 000 and 9000 BP. They were followed by the domestication of foxtail millet-grass in 6000-5000 BP, and common bean, avocado, chili pepper and turkey in 3000-2000 BP.

South America presents the greatest diversity of domesticates. The process was kicked off with the domestication of squash (moschata) around 10000 BP; Root-crop, coca, cotton, chili pepper, manioc and lima beans followed between 9000 and 6000 BP. Peanut, common bean, sweet potato, white potato, quinoa and yam complete the plants repertoire between 5500 and 3500 BP. Were Finally, the llama, alpaca, guinea pig and Muscovy duck were domesticated between 6000 and 2000 BP.

6. Results: Archaeology of African Agro-Systems

Partly because of its straddling position on the equator, Africa presents a virtually symmetric distribution of phyto-geographic zones, with different combinations of environmental settings and plants and animal species. African agro-systems present different and intricate genealogies, and are accordingly the most diverse on earth. The practice of agriculture emerged comparatively late in Africa [49-57]. The earliest remains of cultivated pearl millet (*Pennisetum glaucum*) dated to 4500 BP are documented in the Tilemsi valley. The earliest case of domesticated sorghum (*Sorghum bicolor*) found in eastern Sudan near Kassala is dated to 3500-3000 BCE and African rice (*Oriza glaberrima*) earliest remains are dated to 800 BCE in the In the Inland Niger delta (figure 1). Cultivated non-domesticated sorghum dated to 10-9,000 BP was found in large quantity in several storage pits from the early Holocene village site of Nabta Playa. In contrast, livestock husbandry through the domestication of cattle took place around 10-9,000 BP in the eastern Sahara and spread from there to the mountain ranges of the central Sahara. Hunter-gatherer communities in both northern and southern Africa adopted more intensive forms of predation during the latter Pleistocene [58-60]. They invented the bow and arrow and practiced selective hunting for Barbary sheep in North Africa and Derby's elk in southern Africa. The North African Capsians intensively collect mollusks from the expanses of salt water (Chotts) of the Saharan hinterland. It is in that context that innovations will occur in different parts of the continent.

The West-Asian Neolithic Complex

The West Asian Neolithic complex emerged in the Near East in the Early Holocene. It is based on agriculture and the cultivation of wheat, barley, oats, lentils, flax, and the rearing of goat, sheep, cattle and pork. It spread to the Nile delta, the Fayum depression and from there proceeded West and South. It reached the Ethiopian highlands at an unknown date, probably from the Arabian Peninsula, and overlaps with agriculture based on local plants such as ensete, teff and noog. The Early Neolithic sites of Fayum dates from around 5200 BCE. Fourteen settlements have been identified over 60 kilometers along the north and northeast shores of the lake. The crops of wheat, barley, oats were kept in underground granaries located at a distance from the lake. Mérindé,, inhabited for nearly 600 years from 5000 BCE, is the best-known Early Neolithic site in the Nile Delta. The tradition of a Neolithic mixed economy, combining agriculture and livestock in varying proportions, continues in villages with increasingly elaborate structures, such as El-Omari (4500 BCE) and Ma'adi (3500 BCE).

Another axis of neolithization, also coming from the Near East, but via the Balkans peninsula, followed the European coasts of the Mediterranean, as far West as Portugal. This Neolithic is dubbed "Cardial", the pottery being often decorated with the impression of a shell (*Cardium edule*). Some sites of this axis, such as El-Khril, Achakar, Gar Cahal, and Cal That el Gar, present in Nortern Morocco are mainly rock shelters and caves with seasonal and intermittent occupations.

The Oasis Agro-Complex

The Saharan Oasis complex, a relatively late variant of the West Asian complex that made possible the development of trans-saharan long distance trade networks, is still poorly investigated by archaeologists. It is an intensive form of gardening which requires special hydraulic installations, ensuring permanent access to water, for irrigation and watering purposes (figure 2). It is now known, thanks to the work carried out at the end of the 20th century by Van der Veen in Fezzan, in Libya, that wheat, barley, dates, grapes and figures were cultivated around 700-600 BCE in Zinchecra, an oasis of the Garamantes du 1st millennium BCE. The cultivation of dates then fueled and supported the trans-Saharan trade for centuries.

Figure 2. *Aspects of Saharan Oasis Complex: Ancient foggara being restored in South Tunisia and dates harvest (source: eco-generation.org).*

African Cerealiculture

The cereals domesticated in sub-Saharan Africa are essentially four species of grasses derived from wild varieties - sorgho (*Sorghum* sp.), pearl millet (Pennisetum glaucum), African rice (*Oriza glaberrima*) and fonio (*Digitaria exilis*) cultivated in monoculture and/or in rotation. Sorghum was exploited intensively since the Late Pleistocene, but domesticated varieties appear late in the northeastern portion of the continent, in the Butana Group in Sudan between 3600-3100 BCE (figure 3). DNA sequences extracted from prehistoric sorghums show no difference from those of modern sorghums, suggesting relatively recent domestication. Domesticated sorghum (figure 4) then spread to the rest of the continent and Asia (figure 5). In West Africa, the most reliable sorghum remains, dating to 800 CE, come from Daima, Nigeria. It was the most common cereal in eastern and southern Africa before the arrival of maize in the 16th century (figure 5).

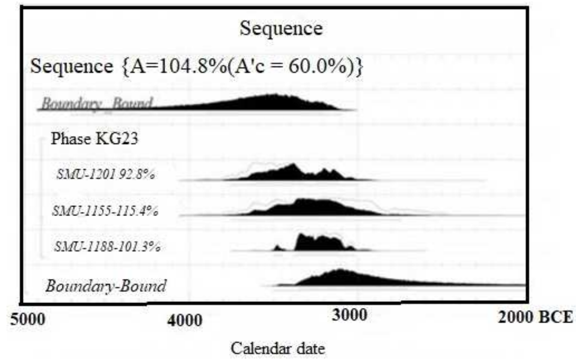

Figure 3. *Chronology of the Earliest domesticated Sorghum specimens (Source: Fuller and Stevens 2018).*

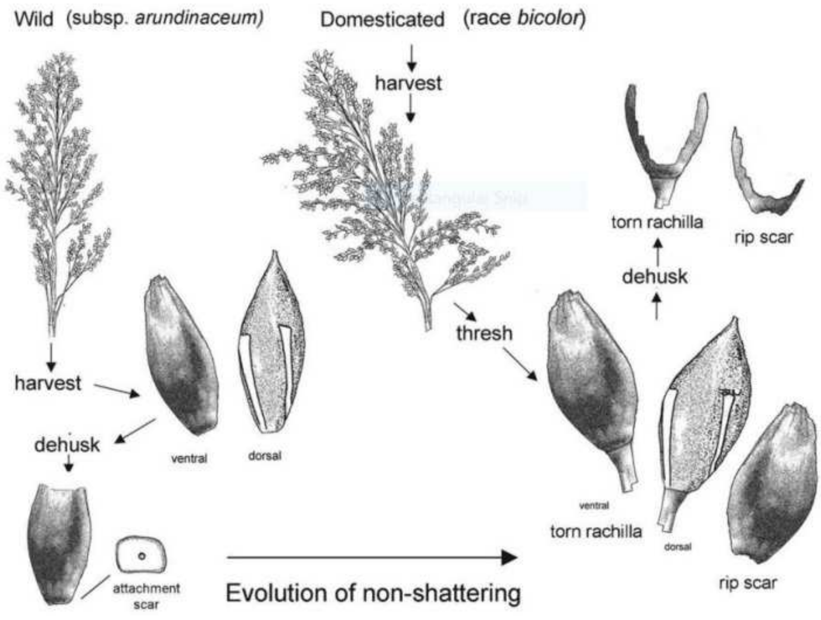

Figure 4. *Wild and Domesticated Sorghum (Fuller and Stevens 2018).*

Domesticated pearl millet remains have been unearthed at several West African sites [61]. They are usually combined with other panicoids, wild rice, fruits and legumes. P. Munson presented a scenario for the domestication of pearl millet in the Dhar-Tichitt region, in the south-western Sahara in Mauritania. The presence in the samples he analyzed of remnants of wild millet suggests local domestication between 2,500 and 1,500 BCE. Pearl millet was also cultivated in the

Kintampo Culture area in present-day Ghana-Ivory Coast during the same period. From 1500 to 1000, it is present in almost the entire Sudano-Sahelian zone, in the Chadian plain, the Nok cultivation area, in northern Burkina Faso, etc. From the end of the 1st millennium BC to the 1st millennium after, the cultivation of millet is adopted throughout sub-Saharan Africa, from the Sahelian zone to southern Africa including the northern fringe of the Equatorial rainforest. It is now clear that pearl millet was domesticated in the Sahara, around the Taoudenni basin in NW Mali around 4240-3090 Cal BCE and from there spread to the rest of the continent and to Asia as will be shown in the case study below.

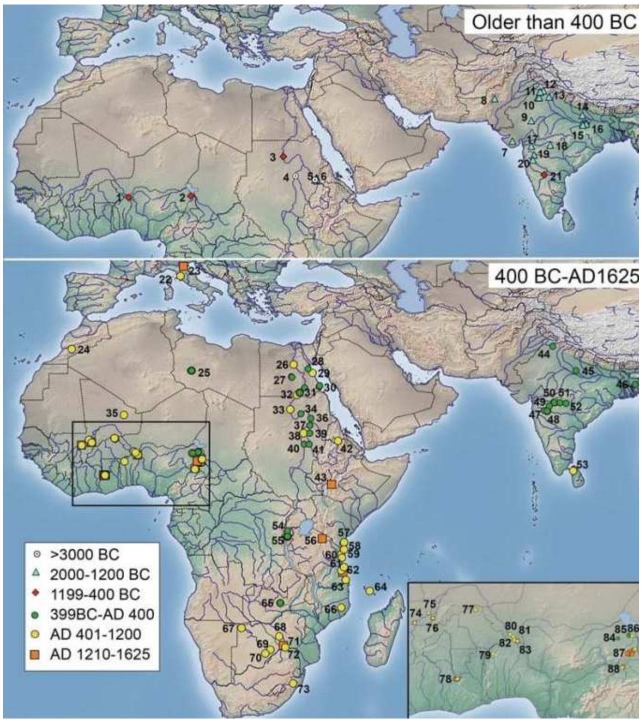

Figure 5. Distribution and Chronology of Sorghum macro-remains in Africa (Source: Fuller and Stevens 2018).

African rice is domesticated in the western part of West Africa. The exploitation of wild rice is documented in a very limited number of sites, in Gajiganna and Kursakata, in the Chadian plain, and Jenne-Jeno, in the interior Niger delta. Remains of domestic rice have been unearthed in levels dated to 300-200 in Jenne-Jeno and 800-700 BCE in Dia, in the floodplain of the Inner Niger Delta. The Gambia Valley, another potential area for domestication of African rice, has so far not been the subject of systematic archaeological research. Choi et al "analysis of whole genome re-sequencing data in the African rice *O. glaberrima* and its wild ancestor *O. barthii* shows that *O. glaberrima* is comprised of at least 5 distinct genetic groups from different areas in West and Central Africa". The domestication of African rice is accordingly non-centric. Its genetic and geographic structure indicates that admixture "allowed local domestication alleles to spread into other proto-domesticated *O. glaberrima* genetic groups in different parts of West and Central Africa".

Figure 6. Charred remains of fonio and cowpeas at Kerebe-Sira-Tomo 4, Burkina Faso.

Fonio, *Digitaria exilis*, a cereal specific to Africa, is cultivated in limited areas, such as the Mouhoun loop, in Burkina Faso, where a significant concentration of charred remains of fonio and cowpeas dated to 1100-1200 CE was recorded at Kerebe-Sira-Tomo 4 (figure 6). White fonio derived from *Digitaria longiflora* its wild progenitor, is a sturdy annual herbaceous C4 plant that is cultivable in a wide range of environmental conditions. It matures fast, in 70-90 days, but has low yields and present residual seed shattering [62-63]. "Fonio has an exceptionally small but very nutritious grain, with both high protein and high dietary fiber content. Fonio can mature in as little as 8 weeks after planting and is commonly grown … on poor quality soils in dry region of the Sudan grasslands and Sahel". It has extensive genetic diversity with a north-south clinal distribution.

Cereals are only part of the diet, which also includes sources of protein and fat from animal and plant sources. Hunting, fishing, and herding provide animal resources. Oil palm, shea, eagle (*Canarium schweinfurthii*) and black-eyed bean provide protein and vegetable fat. Palm nut remains are found in the Kintampo area in Ghana, Obobogo in southern Cameroon, and the megalith area in Central Africa. Shea, now a protected tree, grows in the savannah area. The baobab, also a protected species, provides young shoots, fruits and bark used for making ropes. The black-eyed bean is found in a large area from Senegal to Cameroon. The oldest bean remains come from central Ghana and date from 1830-1595 BCE. There are others in the Oujoungou area, in the Mouhoun loop, and in the Nok culture area. The area of domestication of the black-eyed bean is most likely West African. Sub-Saharan cereal crops have spread to equatorial wetlands, combining and overlapping with equatorial horticultural forms.

7. Pearl Millet Domestication in Macro-Evolutionary Perspective

The genus *Pennisetum* includes 140 species distributed in world's tropical and subtropical regions. It belongs to the subfamily Panicoideae, of the group Paniceae, of the family Poaceae [61-64]. It is comprised of three gene-pools: 1- the primary gene-pool includes the domesticated form *Pennisetum glaucum*, and wild forms *P. glaucum ssp monodii* that cross and have viable seeds and fertile hybrids; 2 - the secondary gene-pool consists of Elephant or Niaper grass, wild relative to *P. glaucum*, *P. purpureum*. They are crossable with pearl millet but have sterile hybrids; and finally, 3 – the tertiary gene-pool that is made of species with strong reproductive barriers, they do not cross with either primary or secondary gene-pools species.

Time and Places of initial pearl millet domestication

The earliest evidence of domesticated pearl found in the Tilemsi Valley in Mali is dated to 4500 BP but inferences from its genomes suggest 4900 BP as the date on initial domestication. The domestication process generates important modification of plants phenotypes. In the pearl millet case, these modifications are manifest through morphological changes common among all cereals: 1) the suppression of spikelet shedding; 2) the reduction in the size of bristles and bracts; 3) the reduction in the number of basal tillers; 3) an increase in seed size; 4) an increase in spikelet pedicel length; 5) an increase in spike length; and finally, 6) the loss of dormancy. J. Clotault *et al* argue “that a category of genes of the flowering pathway were preferentially selected during pearl millet domestication”. Non-shattering of seed was selected over thousands of years. Domesticated pearl millet thus presents less genetic variability than wild sampled forms and their flowering genes display much less variability than random genes (figure 7).

The pathway governing flowering time is critical for crop adaptation and improvement. The phenotypic plasticity of pearl millet, manifest through a wide range of flowering times, has allowed its dispersal and spread to different environmental settings, with the flowering time adjusted to the annual rainfall. “Sahel varieties flower very early (as early as 40 days after planting). Tropical coast varieties flower very late (up to 150 days after planting)”.

Figure 7. *Domesticated pearl millet Pennisetum glaucum (Source: https://world-crops.com/wp-content/uploads/Pearl-millet.jpghttps://world-crops.com/wp-content/uploads/Pearl-millet.jpg).*

Fuller et al examining plant impressions in pottery form sites located in the Taoudenni basin in Malian Sahara, relied on 3 characteristics to chart the evolution of domesticated pearl millet in West Africa: 1)- increase in grain size; 2)- evolution of non-shattering stalked involucres; and 3)- appearance of multiple spikelet involucres. Data from AZ-22 site in Erg-in-Sakane dated to 5500-4950 CalBCE feature wild pearl millet exclusively. Domesticated pearl millet is documented at MT-25 site, Oum el Assel, Erg Chech dated to 4240-3090 CalBCE, and MK 36, Erg Jmeya dated to 3020-1940 CalBCE.

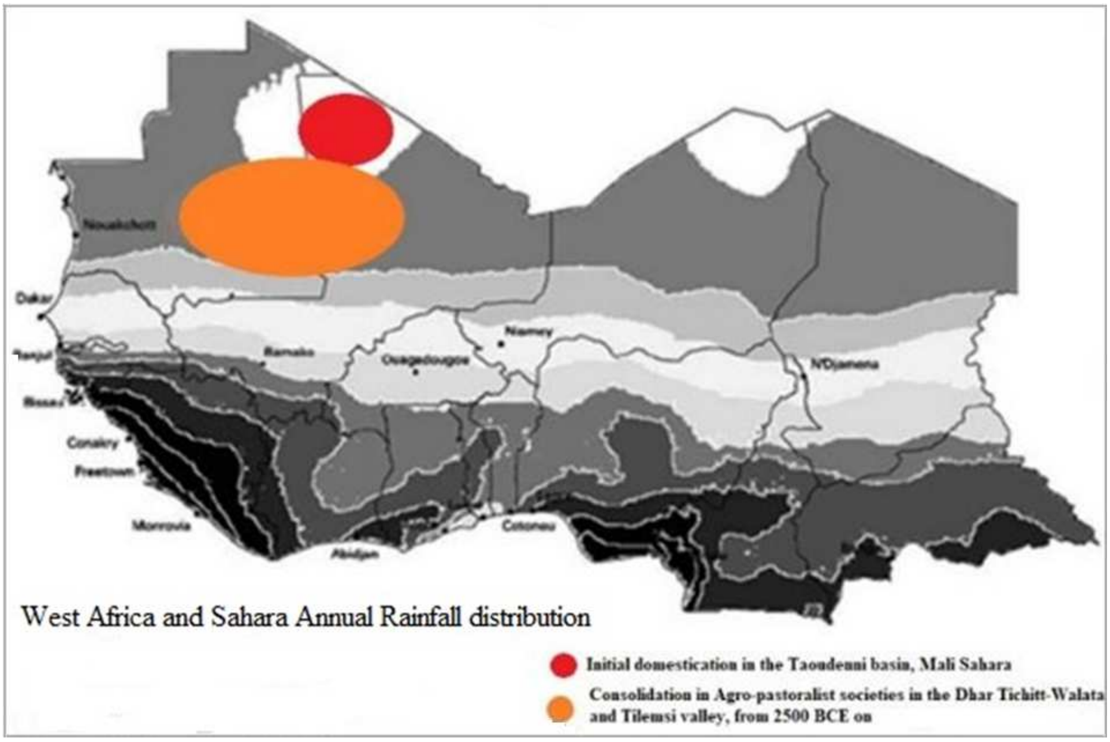

Figure 8. *The location of the area of initial pearl millet domestication in the Sahara in relation to annual rainfall distribution (Modified after Manning et al 2011).*

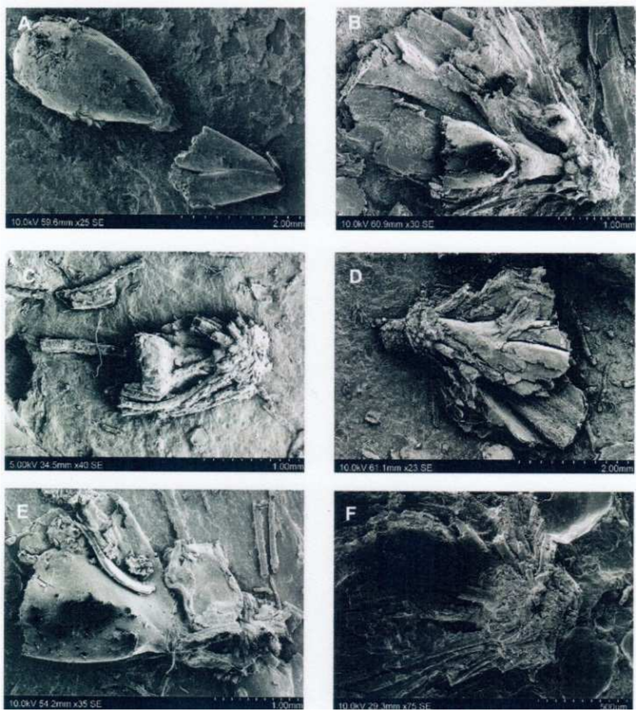

Figure 9. *Pearl millet remains from the Tilemsi valley sites (source: Manning et al 2011).*

Wild pearl millet was intensively exploited in the humid Mid-Holocene Sahara. Average grain size increased by 28% in the 4th millennium BCE with spikelet features preserving wild characteristics. Fully domesticated pearl millet with average seeds' width 38% greater than wild specimens developed in the 3rd millennium BCE. From the initial area of domestication located in the Taoudenni basin in Malian Sahara (figure 8), pearl millet cultivation spread south, in an area stretching from Mali to Mauritania in the Tilemsi Valley (Mali) to the Dhar-Tichitt-Walata-Nema (Mauritania). The botanical macro-remains from the Tilemsi valley sites are dated to 2500 BCE and those form the Dhar Tichitt-Walata-Nema are dated to 2000 BCE. The recorded pearl millet macro-remains from the Tilemsi valley sites feature fully domesticated non-shattering spikelet and seed (figure 9). Manning *et al* show "that pearl millet non-shattering evolved earlier that the start of grain sizes increases".

The Spread of domesticated Pearl Millet

Domesticated pearl millet with increased grain size is present in the Ganges basin in India in the late 2nd Millennium BCE, suggesting that this cereal of African origins spread relatively fast eastward. However, considering the long delay in the establishment of non-shattering genotype and as is the case for the spread of maize in South America, the India specimens could have evolved from partially domesticated isolated progenitor population remotely linked to the West African ones.

In Africa, the spread patterns of *Pennisetum glaucum* is quite straightforward. The earliest domesticated pearl millet macro-remains dated to 4240-3090 BCE are found in the Taoudenni basin in Malian Sahara. Cultivation spread southwest and south, probably linked to the accelerated desertification of the Mid/Late Holocene Sahara to reach the Tilemsi valley in Mali and Dhar Tichitt-Walata-Nema in Mauritania between 2500 and 2000 BCE (figure 4). It then spread south at Winde Koroji and Oujoungou in the Bandiagara (Mali) and Birimu and Boase (Northern Ghana) between 2000 and 1500 BCE. In one and half millennium, from 1500 BCE to the beginning of the Common Era, pearl millet spread some 2000-3000 kms around. It was present in the Libyan Sahara in the north, at Tindra B and Zinchechra; the Middle Senegal valley at Walade in the West; in northern Burkina Faso at Oursi, Ti-n-Akof, and Saouga; in the Chadian plain at Gajiganna, Mege, and Kursakata, the Nok culture area at Janruwa, Janjala, and Akura; and finally in southern Cameroon at Bwambe-Sommet and Abang Minko'o where the savanna grassland expanded at the expense of the equatorial rainforest. During the Common Era, domesticated pearl millet spread to the rest of the continent, in Nubia in the Nile valley, the Great Lakes, East and Southern Africa (figure 10).

From its Sahara-Sahel area of domestication, pearl millet was adopted and spread in different environmental contexts, in Africa and South Asia, displaying directionality, great adaptability and phenotypic plasticity. It was combined to other plants crops - cowpea (*Vigna unguiculata*), yams (*Dioscorea cayenensis*), palm tree (*Elaeis guineensis*) - in distinct food-ways. Humans were clearly the main if not the exclusive dispersal agents, carving new cultural landscapes through land clearing, field preparation, and sustained plant cultivation.

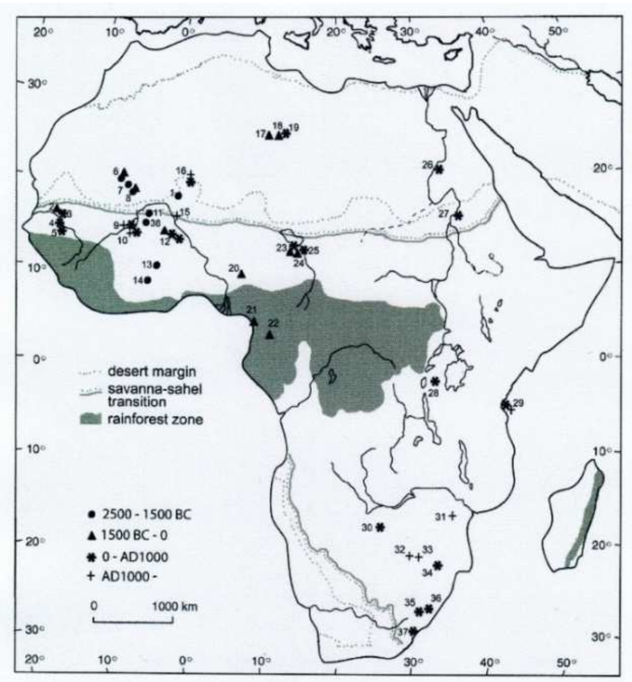

Figure 10. *The expansion of domesticated pearl millet (Source: Manning et al 2011).*

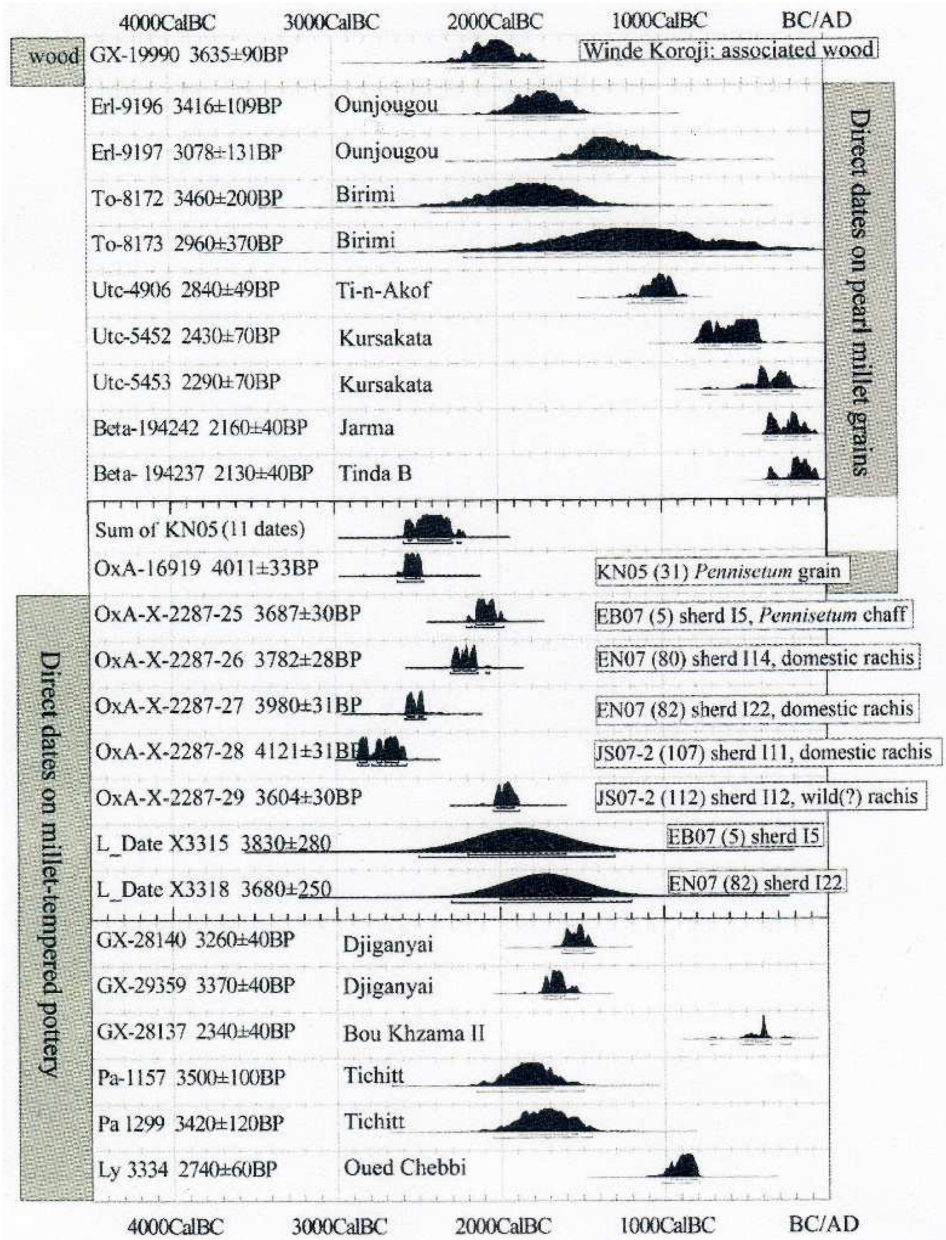

Figure 11. *Radiocarbon dates of Pearl Millet macro-remains (Source: Manning et al 2011).*

8. Discussion: Other Agro-systems

Agricultural practices in the Equatorial forests

Equatorial agro-forestry, horticultural practices combined with the exploitation of protected wild plants, is essentially based on aerial and underground tubers such as yams, in variable combination with oil plants such as oil palm, and / or the elder. The Kintampo cultivation area in West Africa is an interesting case of a combination of cereals and tubers. The “stone graters” or “terracotta cigars” at the Birimu site revealed the presence of yam phytoliths. The "yam belt", which stretches from Togo and Benin in the west to the Central African Republic in the east, is probably one of its likely areas of domestication. The diversity of wild yams is greatest in the forest / savannah transition zone and in gallery forests. The establishment of megalith builders in these regions in the Central African Republic suggests intensive exploitation of wild yams. In addition, the urban civilizations of southern Nigeria, Oyo, Ife, and Benin, as well as the rural forest communities, at Obobogo, along the Congo River, at Igbo-Ukwu, in the equatorial forest, have very likely exploited the yams and wild tubers offered to them by the environment [64].

Crops from Southeast Asia

The East African cereal and horticultural systems of the interior of the continent have been enriched by successive waves of new plants from the Malayo-Polynesian area: sweet bananas, plantains, taro, colocases, rice, etc. According to the accepted scenario, these plants would have been introduced in Africa at the beginning of our era, in the context of the peopling of Madagascar by speakers of Austronesian languages. Recent discoveries have however weakened this scenario, which had the advantage of simplicity. Research carried out on the domestication areas of bananas in the Pacific reveals a more complex situation, with the possibility of multiple origins and several phases of dispersal. The discovery of banana phytoliths dating back to 500 BCE in southern Cameroon suggests a much older date of arrival. Banana phytoliths dated to 3500 BCE recently unearthed in Munsa, Uganda, are reviving the debate. If these data are confirmed, it will be necessary to rethink the genesis of agriculture in Equatorial Africa. Whatever their arrival dates, however, the cultivation of bananas, plantains, taro and other colocases has had a profound impact in the Great Lakes region and had generated an original agrarian landscape with high density population.

New plants from the Americas to modern times

Successive waves of migration and long-distance transfers have introduced new plants to the African continent. The Arab-Muslim expansion brought lettuce, cabbage, turnip, onion, tomato, sugar cane, etc. Sugar cane was the initial impetus of north and west Africans' enslavement in plantations developed by the Portuguese in the Canary Islands in the 15^{th}-16^{th} centuries. American plants were transferred from west to east. In several regions, corn has supplanting sorghum, and cassava is replacing yams. The cocoa tree became an "industrial plant" in Ghana, Cameroon, and Ivory Coast. Many other fruit trees, avocado, papaya, etc., are part of African landscapes today.

In fact, African agro-systems are a patchwork. The oldest complexes absorb the newer ones and produce new syntheses. The combination of plants of West Asian and Ethiopian origin constitutes one of these remarkable syntheses. The ease of cultivation, ease of handling and rates of return generated dynamics specific to each of the complexes examined. Depending on the circumstances, some plants were selected and others abandoned.

9. Conclusion

Research on the neolithization processes range across a broad topic's spectrum including biological, environmental, and behavioral dimensions. Advances in archaeological techniques and methods and genomics through DNA/RNA sequencing technology open new perspectives in domestication research. As featured here with the case study on pearl millet domestication, the EES allows to take into consideration not only "new genetic and archaeological data, but also idea related to epigenetics, plasticity, gene-by-environment interactions, gene culture co-evolution and niche construction", all concepts important to understand selection, phenotypic change, and heritability. The origins of pearl millet domestication has its roots in Middle and Late Holocene pastoral and agro-pastoral systems in Africa. The same genesis probably also applies to the domestication of Sorghum in Eastern Sudan.

Agriculture and livestock husbandry combined in many forms on the African continent during the Neolithic period. Strictly agricultural lifestyles are concentrated in humid equatorial zones while exclusively pastoral systems are located in warm and dry regions as appropriate. The contractions and extensions of these different food production systems were initially governed by climate change. The later intercontinental transfers of animal and plant species and the impact of human communities have generated new combinations, giving rise to highly anthropized landscapes.

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