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# Some Current Topics in Plant Domestication: An Overview with Particular Reference to Amazonia

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## Abstract

Amazonia offers some striking contrasts to better-known regions of the world, notably the Middle East, in which plants were domesticated. These contrasts are pertinent to attempts to formulate general principles of evolution under domestication, particularly now that some of these are being critically re-examined. Topics covered in this paper include a generally applicable definition of plant domestication; how domestication may be recognised archaeobotanically; the relative roles of conscious and unconscious human selection; when and how rapidly domestication occurred; whether the same crop was domesticated more than once; and where a crop was domesticated. The archaeobotanical record for Amazonia and the number of Amazonian crops in which domestication has been critically studied are limited, so detailed comparison with other regions is not yet possible. However, new techniques in archaeology and molecular genetics offer promise that questions that can at present only be posed may become answerable in the not-too-distant future.

## Introduction

Amazonia is now recognised as a region in which plant species were domesticated independently of similar events elsewhere. According to Meyer et al. (2012), 15 species of food crops were domesticated in Amazonia, while Clement et al. (2010) considered that 83 species native to Amazonia or adjacent areas show effects of management, cultivation, or domestication. Some Amazonian domesticates, for example manioc (*Manihot esculenta*), peanut (*Arachis hypogaea*), and pineapple (*Ananas comosus*), are economically important on a global scale while others, such as guaraná (*Paullinia cupana*) and cupuassu (*Theobroma grandiflorum*) are little known outside their native continent. For some, such as manioc and peanut, the probable wild progenitor has been identified. This helps to locate where each was domesticated and to determine what traits have developed through interaction with humans.

For others, such as yautia (*Xanthosoma* sp(p)), arrowroot (*Maranta arundinacea*), and lerén (*Calathea allouia*), the wild species are so poorly known that it is not even certain in which continent of the Neotropics the domesticates were first taken into cultivation.

Amazonia offers a number of significant contrasts with the Middle East, the region on which most discussions of plant domestication have been based. In Amazonia, the domesticated species are mostly perennials (peanut is a notable exception), whereas the staple crops of the Middle East are annuals (wheat, barley, pea, lentil and others). In perennials in general, fewer sexual generations occur in a given period of time than in seed-propagated annuals. This is likely to slow the rate at which variation is generated by genetic recombination and reassortment and hence to slow the pace of evolution under domes-

tication. Amazonian domesticates come from a wide range of plant families, whereas the principal crops of the Middle East come from just two, grasses and legumes. Amazonian crops are therefore likely to show greater diversity in their responses to the selective pressures of domestication.

In these respects, Amazonia provides a potentially useful counterbalance to the Middle East in attempts to formulate general principles of plant domestication. This is particularly pertinent now that several points that were previously widely accepted are being questioned. These include the speed with which domestication occurred, the relative roles of conscious versus unconscious human selection, and the likelihood of multiple independent domestications of the same species. However, to address these questions, it is necessary first to discuss current definitions of domestication and how it may be recognised.

### What is Domestication?

In his two volumes on *The Variation of Plants and Animals under Domestication*, Charles Darwin (1868) never felt it necessary to define domestication. Currently, archaeologists and geneticists both need such a definition, but the diversity of plant species whose variation has been manipulated to varying extents by humans makes it very difficult to produce a “one size fits all” definition.

A generally agreed upon starting point is that domestication results in genetic changes in the features of the organism that constitute its phenotype. These changes occur in response to selection in environments created or modified by humans and make the targets of selection better adapted to these environments and/or to use by humans. The suite of characters affected constitutes the domestication syndrome. “Classic” definitions of domestication thus emphasise features of the individual plant or archaeobotanical specimen.

Individuals live, reproduce, and die, but do not evolve: evolution is an attribute of populations. Evolutionary definitions of domestication, for example that of Clement (1999), therefore describe domestication as a process causing genetic changes in populations such that the average phenotype diverges from the range found in wild populations. Some individuals in populations considered to be domesticated will consequently have the wild phenotype for one or more characters. This applies particularly to populations in early stages of domestication. Fuller (2012) similarly defined a domesticated population as one containing a statistically significant majority of domesticated compared to wild phenotypes. He considered that this would result in the domesticated phenotype becoming irreversibly established in that population. Population-based definitions may cause difficulties in the archaeological recognition of domestication, since archaeobotanical specimens may not be sufficiently numerous to constitute a statistically acceptable sample, or may come from contexts likely to represent a skewed sample because of factors such as post-harvest selection or processing. For example, a midden may contain predominantly discarded specimens rejected by human selection, while storage contexts may contain predominantly specimens favoured by human selection.

Further controversy concerns the relation between cultivation and domestication. Cultivation involves growing plants in conditions involving some degree of protection by humans (tilling the soil; control of weeds, pests, and predators; irrigation). Since cultivation often provides the setting in which domestication occurs, it has been regarded as a prerequisite for domestication (e.g. Gepts 2004). Thus, cultivated plants are not necessarily domesticated, but domesticated plants are always cultivated. However, Casas et al. (2007) showed that, in species ranging from giant cacti exploited for their fruits to weedy herbs gathered as leaf vegetables, selective removal of individuals with less desirable phenotypes and/or introduction of individuals with more desirable phenotypes may change the frequencies of phenotypes, and hence presumably gene frequencies, in manipulated populations without any cultivation. Casas et al. (2007) termed this *in situ* domestication. Amazonia may likewise represent a region in which human manipulation of wild stands of useful species such as fruit trees, combined with discarding or intentional sowing of seeds from individuals with

desirable characters along forest trails or around settlements, could produce populations that are not technically cultivated but in which phenotypic frequencies differ statistically from those in wild populations not manipulated by humans.

Selection in cultivation often produces changes that reduce fitness in natural environments. These include the loss of mechanisms for seed dispersal or loss of mechanical or chemical protection against pests or predators. Clement (1999) therefore added to his definition that domesticated populations can survive only in human-created environments. However, feral cotton and relicts of some other crops can survive in the wild long enough to confuse attempts to locate their original region of domestication. Furthermore, some domesticates, such as peanut, originated from wild progenitors with very restricted distributions, presumably because of specialised ecological requirements and/or limited competitive ability, so it is perhaps not surprising that, outside the limited ranges of their wild progenitors, such crops should be unable to establish in the wild. Definitions that include criteria such as domestication being a response to cultivation or domesticates being unable to survive outside cultivation therefore seem to be over-restrictive.

Additional difficulties occur because wild and domesticated are not alternative states, but end points of a continuum. Clement (1999) recognised the categories of incipient domestication and semi-domestication to cover such intermediate stages. Of 138 crops grown in Amazonia at European contact, he considered 45 to be incipiently domesticated and 41 to be semi-domesticated. These provide an excellent opportunity to study early stages of domestication: an opportunity that has been largely lost for highly domesticated annual seed crops.

### How Did Domestication Occur?

If selection is to be effective in establishing heritable changes that persist across sexual generations, as in domestication, there must be genetic variation for the target characters in the target population. Recently, a distinction has been drawn between domestication genes and diversification genes (e.g. Gross and Olsen 2010). Domestication genes control features of the domestication syndrome, such as loss of dispersal or increase in size. Diversification genes control variants selected after domestication, often relating to different uses of the crop, for example differences between flint, flour, and sweet corn. The domestication syndrome is now frequently regarded as resulting from unconscious selection in the new environment produced by cultivation (e.g. Zeder et al. 2006; Purugganan and Fuller 2011). Genes controlling traits of the domestication syndrome are generally fixed (i.e. invariant) in fully domesticated crops. Diversification genes, on the other hand, control variation within crop species rather than differences between crop and wild populations. They are often targets of deliberate, conscious, human selection, usually after domestication (Zeder et al. 2006).

However, conscious, rather than unconscious, selection for traits of the domestication syndrome seems to be the hallmark of the cases of *in situ* domestication studied by Casas et al. (2007). Thus, individuals of giant cacti with more palatable fruits and/or fewer spines are selectively retained in land cleared for cultivation, while individuals with less desirable phenotypes are eliminated. Similar conscious selection seems likely to have been involved in domestication of many of the tree fruits of Amazonia.

Meyer et al. (2012) found that perennial fruit crops had significantly fewer traits in their domestication syndromes than annual seed crops or vegetatively propagated root crops. This increases the difficulty of distinguishing between domesticated, incipiently domesticated, semi-domesticated, and wild individuals in living species of tree fruits. These difficulties are even more severe when the archaeological record has to be interpreted. Meyer et al. (2012) also found that, when they considered all categories of crop, rather than just annual seed crops, change in secondary metabolites, affecting features such as flavour, toxicity, or pigmentation, was the most common trait associated with domestica-

tion, not loss of dispersal. Some secondary metabolites can be identified in archaeological material. For example, traces of theobromine (one of the alkaloids responsible for the stimulant effects of cocoa and chocolate) have been found in potsherds from Formative sites in Mesoamerica (Powis et al. 2007, 2011). This demonstrated that *Theobroma* seeds were being used much earlier than was apparent from finds of macroremains. Similarly, Reber et al. (2004) used isotope analysis of the long-chain alcohol *n*-dotriacontanol, present in the waxy cuticles of maize kernels, to detect maize in residues in pottery from the east and mid-west of the United States. However, they caution that, where other C<sub>4</sub> plants, such as amaranth, are important in the diet, this marker may not be specific for maize. In a report that leaves various questions unanswered, Powis et al. (2013) reported presence of dihydrocapsaicin, one of the capsaicinoids responsible for the pungency of chile peppers, in residue from a pottery vessel from Mexico. Rather oddly, capsaicin was not found, although, according to the data that they themselves give, capsaicin is three times as abundant as dihydrocapsaicin in pungent peppers. However, if similar methods of extraction and analysis can be critically applied to archaeological chile fruits, it should be possible to determine whether these represent pungent or non-pungent peppers. Likewise, if tests can be devised to detect cucurbitacins in archaeological *Cucurbita* fruits, it should be possible to determine when non-bitter, cucurbitacin-free, hence edible, fruits became established. However, in other crops, flavour is generally due to a complex mixture of chemicals, and it is unlikely that subtle changes in proportions of these will be reliably detectable in archaeobotanical specimens. Many plant pigments break down when exposed to light and/or heat, so changes in colour will be detectable only under particularly favourable conditions of preservation. With present techniques, early signs of domestication in some crops may therefore be missed.

Amongst Amazonian domesticates, the domestication syndrome has been best described for peanut (an annual seed crop) and manioc (a vegetatively propagated perennial root crop). In peanut, most traits of the domestication syndrome listed by Favero and Valls (2009) facilitate harvest of the fruits, which are borne underground and harvested by uprooting the whole plant. Strengthening of the peg (the structure that connects the underground pod to the parent plant), and shortening of both peg and isthmus (the narrow section of pod that separates it into single-seeded segments), so that seeds are borne closer to the parent plant, seem likely to have developed by unconscious selection imposed by harvesting technique, in the same way that sickle harvesting of Middle Eastern cereals resulted in unconscious selection for non-shattering inflorescences. In manioc, selection in cultivation seems to have been more complex. Today, and presumably also in the past, a mixture of conscious, unconscious, and natural selection operates in the plots of subsistence farmers (McKey et al. 2010, 2012). Manioc is propagated vegetatively, by stem cuttings. Choice of genotypes for propagation involves conscious selection, based on features of the tubers, including size, texture, and flavour. Domesticated manioc branches less freely than its wild progenitor, and the stems are therefore thicker. McKey et al. (2012) attributed this to conscious selection for stems with more reserves, which are likely to be more successful as propagules. However, Glémin and Bataillon (2009) pointed out that, under cultivation, space rather than time is a limiting factor in procuring food. This results in selection for plants with a more compact habit that can be grown at greater densities. Unconscious selection for genotypes adapted to close planting could similarly have favoured reduced branching in domesticated manioc. The heterozygosity characteristic of successful clones of manioc seems to be due to both natural and unconscious selection, since less vigorous plants among volunteer seedlings resulting from sexual reproduction are out-competed or not selected for propagation (McKey et al. 2012). These less vigorous plants are more homozygous and show inbreeding depression, whereas more heterozygous genotypes display hybrid vigour, hence are favoured by natural and human selection.

In cases of *in situ* domestication studied by Casas et al. (2007), and probably also in many of the tree crops of Amazonia, most traits of the domestication syndrome developed from pre-existing variation in wild populations. Glémin and Bataillon (2009) suggested that alleles controlling traits characteristic

of domestication could arise and persist in wild populations of outcrossing species, but would be present in very low frequency, if at all, in wild populations of inbreeding species, because of their deleterious effects when homozygous. Domestication of self-pollinating species would thus require a prior period of cultivation, during which appropriate mutations could occur and be selected, whereas domestication of cross-pollinated species could proceed directly by selection on pre-existing variation.

Data with which to test this suggestion are very limited and consequently inconclusive. Maize is an outbreeder, in which branching of plant and ear is controlled to a large extent by the gene *tb1*. Zhou et al. (2011) showed that the maize allele of this gene contains two insertions, which together seem to produce the phenotype of maize rather than that of its wild relative teosinte. Both insertions exist, separately, in wild teosinte populations and probably pre-date domestication. They appear to have been brought together by hybridisation and subsequently fixed by selection under domestication. In contrast, the maize allele of a second important domestication gene, *tg1*, has not been found in any wild teosinte, so is presumed to have originated and been selected during cultivation (Wang et al. 2005). In tomato, which is a facultative inbreeder, the gene with the greatest effect on fruit size is *fw2.2*. The majority of accessions of cherry tomato, the closest wild relative of the domesticated tomato, carry the large fruit allele of *fw2.2*. This may be in part due to hybridisation between domesticated and cherry tomatoes, but Nesbitt and Tanksley (2002) considered that the large fruit allele probably arose before tomato was domesticated. For crops domesticated in Amazonia, candidate genes for traits of the domestication syndrome have usually not yet been identified, so nothing is known about the distribution of “domesticated” alleles of these genes in wild populations, or whether “domesticated” alleles arose before or after the start of cultivation.

### When And How Fast Did Domestication Occur?

In order to study the time element in domestication, domestication must be recognisable in the archaeobotanical record. Meyer et al. (2012) have shown that the classic archaeobotanical markers of domestication, loss of dispersal and increase in size, do not apply to all crops. These markers are most easily studied in macrobotanical remains, but in Amazonia, microbotanical remains (starch grains and phytoliths) are recovered more frequently than macrobotanical specimens. Interpretation of microbotanical remains involves further problems, beginning with that of critical identification. Piperno (2006) distinguished starch grains of domesticated manioc from those of local wild species of *Manihot* in archaeological sites in Panama, but cautioned that among sites within the range of other wild *Manihot* species, comparative studies of these other species would be needed before archaeological starch could be identified as derived from the domesticate. For root crops such as yautia, arrowroot, or lerén, which are less studied than manioc, unravelling their ancestry and establishing the necessary reference collections are major problems. Furthermore, even with adequate comparative material, it is not always possible to identify either starch grains or phytoliths to species: identification to genus or family may be the most that can be achieved. Microbotanical remains are also susceptible to post-depositional movement within a site caused, for example, by downward percolation of rainwater or disturbance by burrowing animals. Starch grains on surfaces of artefacts are generally expected to reflect human food processing or other activities, but Laurence et al. (2011) suggested that modern airborne starch grains could contaminate archaeological tools during excavation. They recommended that air samples be taken during excavation to control for contamination by modern starch rain that could result in incorrect records of prehistoric presence of certain crops.

Phytoliths are inclusions of silica within certain cells of many species of plants and therefore reflect the size of the cell in which they were contained. For *Cucurbita*, size of phytoliths has been used as a criterion of domestication in sites without macrobotanical remains (Piperno et al. 2000, 2009). However, much remains to be learned about the effects of factors other than domestica-

tion on phytolith size. For example, Kistler et al. (2012) showed that, in *Cucurbita pepo*, mean phytolith length in fruits from virus-infected plants was below that of healthy plants, whereas mean length in fruits from plants infected with bacterial wilt was above that of healthy plants. On the evidence of phytoliths alone, wilt-infected wild plants might thus be identified as domesticated, while virus-infected domesticated plants might be identified as wild.

Increased size of phytoliths may be a valid marker of domestication in species where increased size of the harvested organ results from increased size of its constituent cells. However, large fruits of domesticated tomatoes result from increased cell number, not increased cell size (Tanksley 2004). In avocado, increased fruit size is likewise due mainly to increased cell number (Chanderbali et al. 2008), apparently controlled by the avocado homologue of the tomato domestication gene *fw2.2* (Dahan et al. 2010). More studies are needed to establish the relative roles of changes in cell number versus cell size in producing increases in size during domestication.

Establishing the progress of domestication through time requires archaeobotanical samples from different time periods of a size sufficient for statistical analysis. In Amazonia, both macro- and micro-archaeobotanical remains are still too scanty to permit calculation of rates of evolution under domestication. In the Middle East, with a much more abundant archaeobotanical record, Purugganan and Fuller (2010) and Fuller et al. (2012) have attempted such calculations for both cereals and legumes. Many assumptions are involved, some of which may prove to need revision, but their calculations support the conclusion, now becoming generally accepted, that domestication occurred slowly, requiring perhaps 4000 years for annual cereals and 2000 years for annual legumes, rather than the few hundred years suggested by previous models. Evolution in different traits of the domestication syndrome apparently started at different times; for example, grain size in wheat increased before the first indications of loss of seed dispersal, but thereafter loss of dispersal evolved more rapidly than increase in grain size. These findings pose further problems in both the definition and recognition of domestication. Is a crop domesticated as soon as any trait of the domestication syndrome becomes established in the crop population? In other words, are early populations of cultivated wheat with large grains, but still with the ability to disperse their seeds, domesticated or not?

An alternative approach to establishing the time of domestication involves molecular genetics. The degree to which comparable DNA sequences differ in domesticated versus wild lineages may serve to date their divergence. The study of microsatellite variation in maize by Matsuoka et al. (2002) illustrates the possibilities, assumptions, and constraints involved. Their calculations require that the crop had a single origin, from a known progenitor, and that the mutation rate of all microsatellite sequences used is known. Matsuoka et al. (2002) estimated that maize diverged from its wild progenitor, i.e. was domesticated, no earlier than 9188 years ago and probably somewhat more recently. The earliest cobs so far recovered represent fully domesticated maize and are about 6250 years old (Piperno and Flannery 2001), though maize starch and phytoliths have been reported from the early 9<sup>th</sup> millennium BP in Mexico (Piperno et al. 2009). Archaeological and molecular estimates of when maize was domesticated are therefore in surprisingly good agreement.

For crops less well-known genetically than maize and less amenable to experimental determination of mutation rates, use of DNA polymorphisms to calculate times at which lineages diverged involves further assumptions. Mamidi et al. (2011) used computer simulation followed by statistical analysis to find the model of domestication that best fitted sequencing data obtained from parts of 13 nuclear genes of common bean. They concluded that in both Mesoamerica and the Andes, domestication began about 10,000 BP, significantly earlier than the earliest archaeobotanical specimens so far recovered from either region (Kaplan and Lynch 1999). Their simulations included variable mutation rates, since the suggestion that mutation rates can be derived from a single universally applicable molecular clock has proved untenable and calculations of local clocks for particular genes in particular species are fraught with difficulty (Arbogast et al. 2006). However, molecular phylogeneticists are actively interested in dating

branching points in evolutionary trees, and new techniques and/or new methods of analysis are likely to be developed in the not too distant future.

Other studies in what has been termed the archaeogenetics of domestication are also developing rapidly. Early studies of ancient DNA (aDNA) were bedevilled by problems of contamination and degradation of the DNA that had survived. Contamination may be ancient, for example from the fungi and bacteria responsible for decay of the ancient tissues, or recent, for example from human handling. Degraded DNA is often present as short sequences only and other changes may occur that prevent amplification or cause errors in the sequences retrieved (Pääbo et al. 2004). However, recently developed techniques of high throughput DNA sequencing use short stretches of DNA only, so this aspect of degradation of aDNA is not a disadvantage. As many as a few million short fragments of DNA can now be isolated and sequenced in parallel (Delseny et al. 2010; Feuillet et al. 2011). Contaminant sequences can be detected either by an assay before sequencing, which enables the least contaminated specimens to be selected for detailed study (Wales et al. 2012), or after sequencing, when sequences that match those of fungi, bacteria, or other non-target organisms contained in various publicly-available databases are rejected (e.g. Palmer et al. 2012). Studies of aDNA have made possible critical identification of archaeological specimens of non-diagnostic plant parts that could not otherwise be identified beyond the genus. For example, Palmer et al. (2012) studied two samples of cotton seed from Peru. One sample, dated to 800-1000 BP, contained less than 4% cotton DNA, so could not be unequivocally identified to species, but the other, dated 3750 BP, contained 64% cotton DNA and was unambiguously identified as *Gossypium barbadense*. Similarly, Kistler and Shapiro (2011) identified grains of domesticated *Chenopodium* from three different sites in eastern North America, ranging in age from early 4<sup>th</sup> millennium BP to AD 200-900, as all representing an indigenous domesticate, derived from local wild populations, not introduction of domesticated *Chenopodium* from Mexico.

A development yet to be realised on a significant scale is use of a DNA to study evolution and fixation of domestication genes. Jaenicke-Després et al. (2003) studied eleven cobs of maize, ranging in age from about 4300 to 650 years old, and found that all carried the maize allele of the domestication gene *tb1*. The archaeological cobs also carried two alleles present in modern maize for *pbj*, a gene affecting seed storage proteins, and two alleles at *su1*, again alleles that are frequent in modern maize but rare in its presumed progenitor, teosinte. *Su1* affects gelatinisation of starch, hence properties of tortillas and other products made from maize flour. This suggested that kernel quality was an early target of selection. Candidate domestication genes are being identified in an increasing number of crops and sequences of the “domesticated” and “wild” alleles of these genes compared in order to elucidate changes in gene function associated with domestication. Primers could thus be designed to amplify critical sequences of these genes from aDNA. Feuillet et al. (2011) estimated that the cost of sequencing has fallen more than 10,000-fold over the last ten years, so it becomes feasible to study multiple samples, from different parts of the range and different stages of domestication of a crop, in order to gather data on changes in sequence as they relate to possible multiple domestications and possible differences in the start of human selection and times to fixation of genes affecting different traits of the domestication syndrome in a given crop. There are still technical difficulties to be overcome, but the prospects are exciting.

### Was The Same Crop Domesticated More Than Once?

Now that crop domestication is considered to have taken longer than previously thought, researchers are more willing to consider that a given crop may have been domesticated more than once. This is particularly likely when the wild progenitor has a wide geographic range. For example, it is now generally accepted that common and lima beans were each domesticated at least twice, once in Mesoamerica and once in the Andean region. Possible multiple domestications of one crop within a limited region are more controversial. Studies of genome-wide DNA polymorphisms in Old World cereals indicated the expected

single domestication for each crop, whereas genetic control of some traits of the domestication syndrome, some gene sequences, and archaeobotanical data all suggested multiple origins (Burger et al. 2008, Allaby et al. 2010). Various explanations of this contradiction have been proposed. One possibility is that cultivation began many times, but only one lineage of the crop survived to contribute to extant variation (Allaby et al. 2010, Gross and Olsen 2010). Allaby et al. (2010) also suggested that many of the analyses of genome-wide polymorphisms that suggest single domestication are flawed, because they involve construction of dichotomously branching diagrams that cannot show reticulate relationships resulting from hybridisation between different populations. Allaby (2010, Allaby et al. 2010) considered that, during the long period of selection and management preceding full domestication, independent selections from different wild populations would spread in cultivation and this, together with exchange of seeds between different groups of cultivators, would lead to hybridisation or admixture of independently derived crop populations. Computer simulations (Allaby et al. 2008) suggested that, over time, genetic drift combined with human selection would almost always cause all crop populations, whether derived from admixture or not, to be located on the same branch of a dichotomously branched tree, separate from the branch containing the wild populations. This would imply a single origin of the crop. Most investigators therefore now complement analyses that produce dichotomously branched schemes of relationships with analyses such as STRUCTURE (Pritchard et al. 2000) that can show whether a given individual or accession combines genes from more than one source.

Chen et al. (2009) conducted a STRUCTURE analysis of sequence data from four nuclear genes in wild and domesticated avocado. Wild trees were sorted into three clusters that agreed well with the three geographical races long recognised by botanists. Each of these clusters also contained at least one of the cultivars studied, suggesting independent domestication of each geographic race. Anecdotal evidence suggested that other cultivars were of hybrid origin. These were generally assigned to more than one cluster and the assignments generally agreed with their putative parentage, showing that STRUCTURE analysis can potentially detect hybrid origins.

Analyses of DNA sequence data have similarly made a case for two independent domestications of hog plum (*Spondias purpurea*) in Mesoamerica (Miller and Schaal 2005). At least two domestications have been suggested for peach palm in Amazonia (Clement et al. 2010) and for *Capsicum baccatum* in the Andean highlands (Albrecht et al. 2012).

### Where Was A Given Crop Domesticated?

Evidence on where a crop was domesticated comes from three sources. The first is the archaeobotanical record, but in the Americas this is defective in precisely those regions where the staple crops were probably domesticated. For example, manioc was probably domesticated in southwest Amazonia, but the earliest archaeological specimens come from the desert coast of Peru.

The second source of evidence is distribution of wild progenitors, but present distributions may not reflect accurately distribution at the time of domestication, because of climate changes and/or anthropogenic changes such as deforestation, agricultural intensification, or urbanisation.

The third source is molecular evidence. Every crop was domesticated from a limited sample of the gene pool of its wild progenitor. For selectively neutral characters, the crop should therefore retain the genetic fingerprint of the wild population from which it originated. A large number of characters must be used to compensate for possible hitch-hiking of neutral genes along with genes favoured by selection, and also to compensate for possible loss of some variants because of the genetic bottleneck associated with domestication or genetic drift after domestication. Differences in DNA sequences provide the requisite number of characters. However, different genes and also different organelles (nuclei, chloroplasts, and mitochondria) evolve at different rates, so conclusions reached from study of a single gene or organelle may be erroneous. Different sources of

molecular data may agree, in which case the conclusions reached are strengthened, or may disagree, in which case further investigation or explanation of the discrepancy is required.

In manioc, sequencing of parts of three nuclear genes showed that, in each, genetic variation in the crop was almost entirely a subset of the more abundant variation in the presumed wild progenitor, illustrating the bottleneck effect associated with domestication. Haplotypes (nucleotide sequences) in the wild progenitor that matched those of the crop occurred only in southwest Amazonia (Olsen and Schaal 2006). Five microsatellite loci produced similar results (Olsen and Schaal 2001). The agreement between these complementary studies is taken as conclusive evidence on where manioc was domesticated.

Chacón et al. (2005) likewise found more haplotypes, in this case in chloroplast DNA, in wild than in domesticated common bean. Domesticated beans from Mesoamerica and the Andes had the same haplotypes as wild beans from their respective areas, providing further support for the generally accepted view that common bean was domesticated independently in each continent (Gepts and Debouck 1991). Distribution of these haplotypes in wild populations suggested that Andean common bean was domesticated in the general region of southern Peru, Bolivia, and northern Argentina. Analysis of other DNA polymorphisms narrowed this to eastern Bolivia and northern Argentina, suggesting to Beebe et al. (2001) that Andean common bean may have been domesticated in the same region as peanut and spread with peanut, and possibly also with manioc. For Mesoamerica, the chloroplast data suggested that common beans were domesticated in Mexico, possibly more than once, and also in Guatemala. Analyses of other DNA polymorphisms (Beebe et al. 2000) supported independent domestications in Mexico and Guatemala, and possibly also independent domestications in the Mexican highlands and lowlands. On the other hand, Kwak et al. (2009) concluded from analysis of microsatellite data that common beans were domesticated only once in Mesoamerica, near its northwestern frontier.

Chacón et al. (2005) suggested that the discrepancy between these data sets could be resolved if a single domestication in Mexico was followed by “secondary domestications” of local wild beans through hybridisation with domesticated beans spreading in cultivation. Such hybrids would combine traits of domesticated beans with local adaptations from wild beans, since such features are governed by nuclear genes, hence inherited from both parents. However, chloroplasts are maternally inherited, so if wild beans were the female parents in crosses and backcrosses leading to secondary domestication, as seems likely (Papa and Gepts 2003); hybrids would inherit the chloroplast haplotype of the wild population.

As this example shows, molecular data do not necessarily provide unambiguous answers to questions of where or how often any given crop was domesticated, and may indeed suggest more complicated scenarios than were suspected from either morphological or archaeological studies.

## Conclusions

Domestication will always be difficult to define. Human selection has affected different attributes of different crops to different degrees, producing different pathways to domestication and different rates of domestication, both between species and between traits within a single species. To paraphrase a remark that the taxonomist Cronquist reputedly made about species: domestication is like pornography – I can recognise it when I see it, but I cannot define it precisely. Furthermore, in some crops, particularly many fruit crops, domesticated and wild plants are not clearly distinguishable. This problem becomes more acute as one goes back in time.

Domestication retains its significance for students of evolution but, in terms of human history, the beginning of cultivation is probably at least as significant as domestication. Unfortunately, cultivation is more difficult than domestication to detect in the archaeological record.

Questions of how, when, where, and how often crops were domesticated are now subject to two-pronged attack, using new techniques in archaeology and molecular genetics. The new data do not always agree with previously accepted theories, or with each other, but, as Allaby et al. (2010) put it, “both genomes and archaeology contain fragmentary evidence of the past evolution of crops and both must be true ... apparent contradictions mean that we need to re-examine our frameworks of interpretation and analysis ...”

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