

REVIEW

Domestication of Plants in the Americas: Insights from Mendelian and Molecular Genetics

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- **Background** Plant domestication occurred independently in four different regions of the Americas. In general, different species were domesticated in each area, though a few species were domesticated independently in more than one area. The changes resulting from human selection conform to the familiar domestication syndrome, though different traits making up this syndrome, for example loss of dispersal, are achieved by different routes in crops belonging to different families.
- **Genetic and Molecular Analyses of Domestication** Understanding of the genetic control of elements of the domestication syndrome is improving as a result of the development of saturated linkage maps for major crops, identification and mapping of quantitative trait loci, cloning and sequencing of genes or parts of genes, and discoveries of widespread orthologies in genes and linkage groups within and between families. As the modes of action of the genes involved in domestication and the metabolic pathways leading to particular phenotypes become better understood, it should be possible to determine whether similar phenotypes have similar underlying genetic controls, or whether human selection in genetically related but independently domesticated taxa has fixed different mutants with similar phenotypic effects.
- **Conclusions** Such studies will permit more critical analysis of possible examples of multiple domestications and of the origin(s) and spread of distinctive variants within crops. They also offer the possibility of improving existing crops, not only major food staples but also minor crops that are potential export crops for developing countries or alternative crops for marginal areas.

Key words: Domestication syndrome, archaeobotanical record, Mendelian genetics, molecular genetics, quantitative trait loci, American crops.

INTRODUCTION

Domestication is generally considered to be the end-point of a continuum that starts with exploitation of wild plants, continues through cultivation of plants selected from the wild but not yet genetically different from wild plants, and terminates in fixation, through human selection, of morphological and hence genetic differences distinguishing a domesticate from its wild progenitor. These differences constitute the domestication syndrome and generally render the domesticate less capable of survival in the wild, thus dependent on man for its growth and reproduction. Features of the domestication syndrome include loss of dispersal, increase in size (especially of the harvested part of the plant), loss of seed dormancy and loss of chemical or mechanical protection against herbivores.

Crops vary within and between species in their degrees of domestication. All known accessions of *Capsicum pubescens* have large fruits that have lost their dispersal mechanism, and this species occurs only in cultivation. The four other species of domesticated chile pepper each includes a range of variation from wild peppers, through cultivated peppers with somewhat larger fruits that are still capable of natural dispersal, to fully domesticated peppers with large fruits that remain firmly attached to the parent plant after maturity. 'Domesticated' may therefore describe an

entire species, or just some of the variants within a species. Where there is intraspecific variation in the degree of domestication, it is possible to study the genetic control of traits of the domestication syndrome in segregating generations of appropriate intraspecific crosses.

Vegetatively propagated root crops and perennial fruit crops show fewer features of the domestication syndrome than annual seed crops, and domestication may occur more slowly because fewer sexual generations occur in a given period of time. Clement (1999) proposed two intermediate categories, incipiently domesticated and semi-domesticated, to cover the spectrum of changes resulting from human interactions with species of tree fruits in Amazonia. Semi-domesticated also fits the situation described by Casas *et al.* (1999) for *Stenocereus stellatus*, a giant cactus exploited and cultivated for its fruit in the Tehuacán Valley of Mexico. Some plants in home gardens have fruits with pulp of colours not recorded in the wild, and most have sweet fruit whereas most wild plants have sour fruit. Wild and cultivated populations differ statistically in various characters likely to be targets of human selection, though some cultivated plants are morphologically indistinguishable from some wild plants. Cultivated populations are thus not genetically fixed for any characters distinguishing them from wild populations, but frequencies of alleles governing the characters subject to human selection presumably differ. Casas *et al.* (1999) considered that such changes in allele frequencies resulting from human selection constitute at least incipient domestication.

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Gepts (2004) considered cultivation a necessary but insufficient condition for domestication. However, domestication (or at least incipient or semi-domestication) without cultivation may occur by selective removal of undesirable phenotypes and/or enhancement of desirable phenotypes in wild populations, thus changing the proportion of phenotypes in the managed populations, as described by Casas *et al.* (1997, 1999) and Anderson (2004) for various species. Casas *et al.* (1997) noted that in open- or cross-pollinated species, selective retention of desirable phenotypes in managed populations will promote mating between these plants. More progeny will then show the desired characters, leading eventually to fixation of these characters. Casas *et al.* (1997) termed this *in situ* domestication and suggested that, since *in situ* management of wild and weedy species is very common in Mesoamerica, *in situ* domestication may also have occurred frequently and may explain how various outbreeding species became some of the first domesticates in this region, in contrast to the Middle East, where most of the early domesticates are inbreeders (Zohary, 1984).

Despite difficulties in defining domestication, most workers agree that there were several independent regions of plant domestication in the Americas and that, quite frequently, different species of the same genus were domesticated independently, in different regions and by different peoples. More rarely, the same species was domesticated more than once, in different parts of the range of a widespread wild progenitor. These different, but congeneric (or conspecific), domesticates show similar changes resulting from human selection. This raises the question of whether their similar phenotypes are produced by similar genotypes, or whether selection in different environments, by humans of different cultural backgrounds, exerted on progenitor populations that differed genetically, resulted in different genetic pathways to the domesticated phenotype. In the latter event, different domesticated genotypes could perhaps be combined to produce a 'super-domesticate'. The rapidly developing techniques of molecular genetics are providing tools with which to investigate these and other questions, though questions still outnumber answers.

The Americas have contributed a number of crops of major global importance, for example maize (*Zea mays*), potato (*Solanum tuberosum*), cassava (*Manihot esculenta*) and common bean (*Phaseolus vulgaris*). In many cases, other species in the same families or genera are or have been used, sometimes quite intensively, but were never fully domesticated or have remained only minor crops. Better understanding of the molecular and/or genetic basis of domestication may suggest ways of improving these crops, either for local subsistence or as 'new' crops with commercial or export potential.

REGIONS OF PLANT DOMESTICATION IN THE AMERICAS

Four regions are now generally considered to have been independent areas of crop domestication in the Americas: eastern North America, Mesoamerica, the Andean region

and the tropical lowlands of South America. Table 1 shows the approximate dates of the first appearance in the archaeological record of some of the cultigens associated with each region.

Eastern North America

Only four species are currently regarded as having been domesticated in eastern North America (Smith, 2006), far fewer than the number of species domesticated in the other regions. The eastern North American domesticates also appear later in the archaeological record than the first domesticates in the other regions.

Rivers in eastern North America provided abundant fish and shellfish, while gathered nuts were the primary plant staple (Watson, 1989). *Cucurbita pepo* ssp. *ovifera* was apparently the first domesticate, possibly because its fruits were useful as containers and fishnet floats, though the oil-rich seeds may have been eaten (Asch and Hart, 2004). Vegetable forms (crookneck, acorn and scallop squashes) developed later. *Iva annua* (marshelder) and *Helianthus annuus* (sunflower) were also domesticated for their oil-rich seeds. The first sign of domestication in all three is the appearance of large seeds or fruits, outside the range of modern wild forms (Smith, 2006). *Cucurbita pepo* and sunflower are still important crops, but marshelder had disappeared from cultivation by the time of European contact (Asch and Asch, 1978). Seeds of the fourth domesticate, *Chenopodium berlandieri*, are not significantly larger than those of wild chenopods but do have thinner testas (Smith, 1984), presumably reflecting loss of seed dormancy. This species survived as a crop plant until the 18th century (Smith, 1995) but is now only a weed. Other species thought to have been cultivated but not showing any morphological changes indicative of domestication include *Polygonum erectum*, *Ambrosia trifida*, *Phalaris caroliniana* and *Hordeum pusillum* (Asch and Hart, 2004). Wild rice (*Zizania palustris*) and Jerusalem artichoke (*Helianthus tuberosus*) were exploited, but may owe their domestication to Europeans.

The eastern North American seed crops were apparently harvested by cutting or uprooting (Gremillion, 2004). Both techniques are expected to favour loss of seed dispersal (Davies and Hillman, 1992). This has not been documented for most of the putative cultigens of eastern North America, possibly because the plant parts that would show these changes are not usually recovered in archaeological samples of harvested seeds or fruits. Increased size of seeds, which in many Old World crops precedes loss of dispersal (Fuller, this issue), also has not occurred in many of these putative cultigens, perhaps because they were, at least initially, grown simply for supplementary subsistence, to buffer the effects of non-mast years in the wild nuts (Gremillion, 2004). Modern wild populations of *I. annua*, *C. berlandieri* and *P. erectum* have grain yields comparable with those estimated for prehistoric North American maize (Smith, 1989). Human selection pressures on such productive but subsidiary crops might well have been too limited to bring about any marked changes in phenotype. In eastern North America, therefore, potential crop

TABLE 1. *Regions of plant domestication in the Americas and approximate dates of first appearance in the archaeological record (years before present, uncalibrated) of some of the species domesticated in each region (species marked with an asterisk have not been recorded archaeologically)*

Years before present	Eastern North America	Mesoamerica	Andean region	Tropical lowland South America
	<i>Helianthus tuberosus</i> * <i>Zizania palustris</i> *	<i>Chenopodium berlandieri</i> ssp. <i>nuttalliae</i> * <i>Pachyrhizus erosus</i> * <i>Phaseolus lunatus</i> (d) ¹³	<i>Physalis peruviana</i> * <i>Solanum quitoense</i> * <i>Pachyrhizus ahipa</i> (d) ²⁶ <i>Nicotiana tabacum</i> (d) ¹⁶	<i>Ananas comosus</i> * <i>Solanum sessiliflorum</i> *
1000		<i>Phaseolus coccineus</i> (d) ¹³ <i>Phaseolus acutifolius</i> (d?) ¹³	<i>Amaranthus caudatus</i> (d) ¹⁷ <i>Solanum muricatum</i> (d) ²¹	
2000	<i>Polygonum erectum</i> (c) ¹ <i>Hordeum pusillum</i> (c) ¹ <i>Phalaris caroliniana</i> (c) ¹	<i>Phaseolus vulgaris</i> (d) ¹³ <i>Canavalia ensiformis</i> (d) ¹⁷ <i>Persea americana</i> (d?) ²⁴ <i>Theobroma</i> sp. (?cacao) (d?) ¹²	<i>Pachyrhizus tuberosus</i> (d) ²⁵	
3000	<i>Chenopodium berlandieri</i> ssp. <i>jonesianum</i> (d) ²³		<i>Oxalis tuberosa</i> (d) ¹⁰ <i>Erythroxylon novogranatense</i> ¹⁶	
4000	<i>Iva annua</i> (d) ²³ <i>Helianthus annuus</i> (d) ²³ <i>Cucurbita pepo</i> ssp. <i>ovifera</i> (d) ²³	<i>Amaranthus cruentus</i> (d) ¹⁷ <i>Amaranthus hypochondriacus</i> (d?) ¹¹ <i>Physalis</i> sp. (c?) ¹¹	<i>Phaseolus vulgaris</i> (d) ¹³ <i>Chenopodium quinoa</i> (d) ⁴ <i>Cucurbita maxima</i> (d) ¹⁴ <i>Solanum tuberosum</i> (d) ¹⁶ <i>Ipomoea batatas</i> (d) ¹⁶ <i>Canna edulis</i> (d) ¹⁷ <i>Capsicum baccatum</i> (d) ¹⁷	<i>Capsicum chinense</i> (d) ¹⁶
5000	<i>Ambrosia trifida</i> (c) ¹	<i>Cucurbita argyrosperma</i> (d?) ²² <i>Gossypium hirsutum</i> (d) ¹⁷ <i>Capsicum annuum</i> (d?) ⁵ <i>Setaria parviflora</i> (d?) ²	<i>Cucurbita ficifolia</i> (d) ¹⁴ <i>Cucurbita moschata</i> (d) ¹⁴ <i>Gossypium barbadense</i> (d) ¹²	
6000		<i>Zea mays</i> (d) ¹⁸ <i>Cucurbita moschata?</i> (d) ^{14, 21} <i>Zea mays</i> (d) (pollen, phytoliths) ³		<i>Manihot esculenta</i> (d) ^{6, 8} <i>Maranta arundinacea</i> (starch grains) ⁸
7000		<i>Setaria macrostachya</i> (c?) ² <i>Cucurbita pepo</i> ssp. <i>pepo</i> (d) ²²	<i>Cucurbita moschata</i> (d) ⁹	<i>Arachis hypogaea</i> (d) ⁹ <i>Calathea</i> sp. (phytoliths) ¹⁹ <i>Maranta</i> sp. (phytoliths) ¹⁹

d, domesticated; c, cultivated.

¹Asch and Hart (2004); ²Austin (2006); ³Blake (2006); ⁴Bruno (2006); ⁵Buckler *et al.* (1998); ⁶Chandler-Ezell *et al.* (2006); ⁷Damp *et al.* (1981); ⁸Dickau *et al.* (2007); ⁹Dillehay *et al.* (2007); ¹⁰Emshwiller (2006); ¹¹Fritz (1995); ¹²Hurst *et al.* (2002); ¹³Kaplan and Lynch (1999); ¹⁴Merrick (1995); ¹⁵Pickersgill (1969); ¹⁶Pickersgill (2006); ¹⁷Pickersgill and Heiser (1977); ¹⁸Piperno and Flannery (2001); ¹⁹Piperno and Pearsall (1998); ²⁰Piperno and Stothert (2003); ²¹Prohens *et al.* (1996); ²²Smith (2005); ²³Smith (2006); ²⁴Smith (1966); ²⁵Towle 1961; ²⁶Ugent *et al.* (1986).

species, other than the four domesticates, seem to have remained at the stages of cultivation or incipient domestication.

Mesoamerica

The most extensive archaeobotanical sequences in Mesoamerica come from ecological settings unsuited to the wild progenitors of the major Mesoamerican crops (Buckler *et al.*, 1998). These crops thus appear in the archaeobotanical record as fully domesticated, and the selective pressures imposed early in their domestication are unknown.

As in eastern North America, *Cucurbita* is the earliest domesticate. Mesoamerican domesticated *C. pepo* is now assigned to a different subspecies from the North American domesticate (Decker, 1988). Data from isozymes and chloroplast, mitochondrial and DNA polymorphisms all indicate that the two subspecies were domesticated independently (Decker, 1988; Wilson *et al.*, 1992; Decker-Walters *et al.*, 2002; Sanjur *et al.*, 2002). A second species, *C. argyrosperma* (syn. *C. mixta*), was probably domesticated in the hot lowlands of southern Mexico (Merrick, 1995). *Cucurbita moschata*, which includes the butternut squash, is closely related to but specifically distinct from *C. argyrosperma*. Its wild ancestor is unknown but it may have been domesticated in northwestern South America rather than, or as well as, in Mesoamerica (Merrick, 1995).

Macrobotanical remains suggest that maize was domesticated later than *Cucurbita* (Piperno and Flannery, 2001), though this may change if/when archaeological investigations are conducted closer to the presumed region of domestication of maize, the Balsas basin of west central Mexico. Microbotanical remains (starch grains, phytoliths and pollen) from sites in Central America and northern South America antedate the earliest macrobotanical remains from Mexico (Piperno and Pearsall, 1998; Dickau *et al.*, 2007), and Matsuoka *et al.* (2002) calculated from mutation rates in microsatellites that maize diverged from its presumed wild progenitor about 9000 years ago. If these dates hold, the suggestion that maize displaced some earlier grain crops, notably *Setaria parviflora* (Austin, 2006), may need to be revised.

Beans were apparently domesticated later than maize and *Cucurbita* (Kaplan and Lynch, 1999): common bean (*Phaseolus vulgaris*) in central Mexico (Gepts and Debouck, 1991; Chacón *et al.*, 2005), the drought-adapted tepary bean (*P. acutifolius*) in central or northern Mexico (Muñoz *et al.*, 2006), the runner bean (*P. coccineus*) in the cool humid highlands (Debouck and Smartt, 1995) and the sieva bean (small-seeded *P. lunatus*) in the humid lowlands of either Mexico or the eastern side of the Andes (Gutiérrez-Salgado *et al.*, 1995). A fifth species, *P. dumosus* (syn. *P. polyanthus*), not recognized in the archaeological record, may have been domesticated in Guatemala (Debouck and Smartt, 1995).

Records of tributes paid to the Aztec emperor show that the pseudocereals (*Amaranthus* spp. and possibly also *Chenopodium*) ranked not far behind maize and beans

(Sauer, 1950; Wilson and Heiser, 1979). *Amaranthus cruentus* and *A. hypochondriacus* were domesticated from a complex of weedy forms whose relationships with the crop (wild progenitors, feral derivatives or contributors of new characters by introgression) are still unclear (Sauer, 1967; Hauptli and Jain, 1984). *Chenopodium berlandieri* ssp. *nuttalliae* was domesticated from Mexican wild *C. berlandieri* (Wilson and Heiser, 1979), probably independently of domestication of *C. berlandieri* in eastern North America (Smith, 2006). There is as yet no archaeobotanical record of domesticated *C. berlandieri* in Mesoamerica, but it has been cultivated for long enough in Mexico to have evolved into a multipurpose crop, with different forms grown as a leaf vegetable, a broccoli-like vegetable and a grain crop (Wilson and Heiser, 1979).

The only root crop definitely domesticated in Mexico is the yam bean (*Pachyrhizus erosus*), a legume grown for its fleshy roots and now gaining popularity in the USA and elsewhere (National Research Council, 1989). Sweet potato (*Ipomoea batatas*) may have been domesticated in Mesoamerica, but its centre of origin is still not definitely known.

Other Mexican domesticates add variety to the diet without being major sources of calories. The chile pepper of the Mesoamerican highlands, *Capsicum annuum*, is today the most important species of *Capsicum* on the world scale. Tomato appears to have been domesticated in Mesoamerica later than many other crops, possibly following the spread of its weedy ancestor, the cherry tomato, from western South America as a weed of agriculture (Jenkins, 1948). It was probably preceded in cultivation by the Mexican green tomato, *Physalis philadelphica* (Jenkins, 1948). Cacao (*Theobroma cacao*) seems also to have been domesticated in Mexico following natural or possibly human-mediated spread from South America (Whitkus *et al.*, 1998; Motamayor *et al.*, 2002).

Fibres, like containers, were important non-food plant products in prehistoric economies. *Gossypium hirsutum*, the most productive of the modern cottons, was probably domesticated in the Yucatán peninsula from the local wild *G. hirsutum* (Brubaker and Wendel, 1994).

Andean region

As in Mesoamerica, the most extensive archaeobotanical record comes from an area in which few crops are likely to have been domesticated, in this case the desert coast of Peru. Relatively few excavations have been undertaken in the Andean highlands, where the closest wild relatives of many Andean domesticates occur.

The first plants domesticated once again appear to have been various species of *Cucurbita*, not surprising since the early archaeobotanical records mostly come from pre-pottery maritime peoples who would have needed both containers and fishnet floats. Macroremains of four different species appear between 4000 and 5000 years ago. The wild ancestor of *C. maxima* is today confined to Bolivia, Argentina and Uruguay (Sanjur *et al.*, 2002), the wild ancestor of *C. ficifolia* is unknown but this species is assumed to be an Andean domesticate (Andres, 1990),

while *C. moschata* is a lowland-adapted species whose wild ancestor is also unknown (Merrick, 1995). *Cucurbita ecuadorensis* may never have been more than a semi-domesticate subsequently replaced by *C. moschata* (Piperno *et al.*, 2000).

Unusually, no major cereal was domesticated in the Andes. *Bromus mango*, a minor cereal domesticated in Chile, became extinct in historic times (Hammer, 2003). Macrobotanical remains of maize have been reported in the archaeological record in South America at about the same time as the earliest macrobotanical remains of maize from Mexico (Bonavia and Grobman, 1989; Shady, 2006). Microbotanical remains suggest maize reached South America even earlier (Piperno and Pearsall, 1998; Pearsall *et al.*, 2004; but see also Blake, 2006). No close wild relative of maize is known in South America, and microsatellite data suggest a single domestication of maize in Mesoamerica (Matsuoka *et al.*, 2002) followed by spread to South America. The indigenous carbohydrate staples in the Andean region were not cereals, but pseudocereals and ‘root’ crops grown for their underground storage organs.

The principal pseudocereal in the Andes is quinoa (*Chenopodium quinoa*). This is a tetraploid, like the Mesoamerican and North American domesticated *C. berlandieri*, but the two species are clearly distinct (Wilson and Heiser, 1979). Quinoa was domesticated in the Andes from conspecific wild or weedy progenitors (Wilson, 1990). The cold-tolerant cañihua (*C. pallidicaule*), found at the upper limits of crop cultivation in the Andes, is a semi-domesticate that retains many features of its wild progenitor (Gade, 1970). The Andean grain amaranth, *Amaranthus caudatus*, is, like quinoa, thought to have been domesticated from an Andean progenitor (*A. quitensis*) independently of the domestication of grain amaranths in Mesoamerica (Sauer, 1967) though the taxonomy of both weedy and domesticated amaranths is still confused, and a single domestication remains possible (Hauptli and Jain, 1984).

Although the Andean region is traditionally associated with seed crop agriculture, ‘root’ crops grown for their starch-rich vegetative storage organs were and are important at both low and high altitudes. Principal among these is potato (*Solanum tuberosum*), domesticated in the highlands of southern Peru (Spooner *et al.*, 2005). Other highland domesticates, little known outside the Andes, include oca (*Oxalis tuberosa*), ullucu (*Ullucus tuberosus*) and ñu (*Tropaeolum tuberosum*). Achira (*Canna edulis*) and sweet potato do not tolerate low temperatures so are grown at lower altitudes.

Vegetative storage organs are notoriously poor in protein and, in the Andean region, as in Mesoamerica, significant amounts of dietary protein come from legumes. Common bean and lima bean both have wild ancestors that range from Mesoamerica south along the Andes. Data on seed storage proteins, isozymes and DNA polymorphisms all indicate that both species were domesticated at least twice, in the Andean region and in Mesoamerica (Gepts and Debouck, 1991; Gutiérrez-Salgado *et al.*, 1995; Chacón *et al.*, 2005). Andean jack beans are treated as a

species distinct from the Mesoamerican domesticate (*Canavalia plagiosperma*, as opposed to *C. ensiformis*), though the two are sufficiently closely related to hybridize (Sauer, 1964) and may have differentiated as a result of geographic isolation following spread from a single centre of domestication. The Andean yam bean, *Pachyrhizus ahipa*, produces a fleshy root very similar to that of the better-known Mexican *P. erosus*, but today is confined to a very limited part of the Andes in Peru and Bolivia (Sørensen, 1988).

Many of the fruits cultivated or exploited in the Andean region are little known outside this region, but the golden-berry or Cape gooseberry (*Physalis peruviana*) is now a minor export crop in Colombia, the pepino or melon pear (*Solanum muricatum*) and the tree tomato (*Solanum betaceum*, syn. *Cyphomandra betacea*) have been grown for export in New Zealand, and the naranjilla (*Solanum quitense*) has attracted attention as an underexploited crop (Heiser and Anderson, 1999).

Chile peppers have been consumed in the region for over 5000 years (Pickersgill, 1969; Perry *et al.*, 2007). *Capsicum baccatum* was probably domesticated in the valleys of Bolivia south of the Amazon watershed, but the wild ancestor of the highland species *C. pubescens*, and hence its centre of domestication, are not known. The Andean region is also the centre of origin of two well-known stimulants, coca (*Erythroxylon coca* and *E. novogranatense*) and tobacco (*Nicotiana tabacum* and *N. rustica*).

Cotton is one of the earliest plants to appear in the archaeobotanical remains from coastal Peru and was used for fishing lines and nets, as well as textiles. South American domesticated cotton belongs to a different species, *Gossypium barbadense*, from Mesoamerican *G. hirsutum*, and appears to have been domesticated from local wild forms (Stephens, 1973; Westengen *et al.*, 2005).

Tropical lowland South America

The Amerindian population of Amazonia has been estimated as at least 5 million at the time of European contact (Clement, 1993). They subsisted by hunting, fishing and the cultivation, management or enhancement of at least 138 plant species in 44 families (Clement, 1999). Archaeological investigations in Amazonia are still very limited, but cultigens domesticated in the lowlands east of the Andes have been recovered from archaeological sites on the Pacific coasts of Peru and Ecuador. The dates of these specimens give a minimum estimate of the antiquity of Amazonian agriculture.

Tropical lowland South America is traditionally viewed as a centre of root crop horticulture. The most important of these crops, today and prehistorically, is cassava (*Manihot esculenta*), which was domesticated on the southern border of Amazonia (Olsen and Schaal, 2006). Similar studies have not yet been conducted to locate the sites of domestication of arrowroot (*Maranta arundinacea*) or cocoyam (*Xanthosoma sagittifolia*). Llerén (*Calathea allouia*) which, on the evidence of phytolith studies, was widespread prehistorically (Piperno and Pearsall, 1998), is

today a minor and probably disappearing cultigen, as is the American yam (*Dioscorea trifida*).

Clement (1993) has emphasized that cassava is unsuitable as a staple because of the limited protein content of its tubers. Some dietary protein was undoubtedly provided by maize, which was widely cultivated at the time of European contact. Clement (1999) noted that one of the early European explorers also recorded 'much oats', with which the Indians made bread, and suggested that this may have been the grass *Leersia hexandra*, though Vaughan considers that it was more probably *Oryza glumaepatula* (D. A. Vaughan, National Institute of Agrobiological Sciences, Japan, pers. comm.).

One important legume, the peanut or groundnut (*Arachis hypogaea*), a tetraploid annual, was domesticated east of the Andes, probably close to the area in which cassava was domesticated (Kochert *et al.*, 1996). It became widespread prehistorically, possibly spreading in association with cassava. In contrast, *A. villosulicarpa*, a diploid perennial cultigen in a different section of the genus, is confined to a single Amazonian tribe (Galgaro *et al.*, 1997). A third species of yam bean, *Pachyrhizus tuberosus*, is still widely cultivated in Amazonia and may have been domesticated in western Amazonia, though Sørensen (1988) suggested that it may not be specifically distinct from the Mesoamerican *P. erosus*.

Pineapple (*Ananas comosus*) is the most familiar of the fruits domesticated in Amazonia. Many species of palm are valued for their fruits, but Clement (1993) considered that only pejobaye or peach palm (*Bactris gasipaes*) is truly domesticated. Its starchy fruits are eaten cooked and also provide flour for baking (Clement, 1993). Cocona (*Solanum sessiliflorum*) is related to the Andean *S. quitoense* and similarly used mainly for juice (Heiser, 1985). The pulp around the seeds of cupuaçu (*Theobroma grandiflorum*) also yields a delicately flavoured juice, much valued locally (Smith *et al.*, 1992).

Capsicum chinense is better adapted to hot humid conditions than the other domesticated chile peppers. It is thought to have been domesticated in the lowlands east of the Andes and to have spread in association with cassava and perhaps peanut (Pickersgill, 1969).

CHANGES ASSOCIATED WITH DOMESTICATION

Schwanitz (1966), Purseglove (1968) and Hawkes (1983), among others, have provided comprehensive treatments of the changes occurring under domestication, so discussion here will centre on data gathered since these reviews.

Loss of dispersal mechanisms

This often involves loss of an abscission zone from some part of the plant. Modern cultivars of American wild rice and maize have lost the abscission zones within the inflorescence which cause shattering in their wild relatives. Fruits of wild chile peppers separate easily from the receptacle at maturity, while fruits of domesticated peppers remain firmly attached to the plant. In tomato, the abscission

zone is in the pedicel, and wild-type abscission has been lost only in processing tomatoes, i.e. relatively recently and through the action of tomato breeders (Mao *et al.*, 2000). Successful abscission involves formation of an abscission zone differentiated from the surrounding tissues, followed by separation of cells in this zone.

However, loss of dispersal does not always involve loss of an abscission zone. The indehiscent pods of domesticated common bean result from loss of fibres in the sutures and walls of the pods (Koinange *et al.*, 1996). In wild chenopods, the persistent perianth opens to reveal and release the mature fruit, whereas in the domesticates the perianth encloses and retains the grain even when it is fully ripe. The involucre bracts of wild vs. domesticated sunflowers behave in a similar way (C. B. Heiser, Indiana University, USA, pers. comm.).

Some crops grown for and propagated by underground organs likewise have less efficient dispersal of these organs than their wild relatives. In *Arachis*, the fruits develop underground because a meristem at the base of the ovary becomes active after fertilization and produces a positively geotropic peg which implants the fruit in the soil. In wild peanuts, after the fruit has been implanted, the peg may extend horizontally for more than a metre, while an additional meristem within the fruit produces a narrow isthmus, sometimes several centimetres long, which breaks easily and separates the pod into single-seeded segments (Gregory *et al.*, 1973). In domesticated peanuts, the isthmus is virtually non-existent and the peg is shorter and tougher so the fruits are borne closer to the parent plant and can be harvested by uprooting. Similarly, in domesticated potatoes, the stolons are shorter than in the wild species, so the tubers are borne closer to the parent plant (Hawkes, 1983).

Increase in size

This is usually especially marked in the part of the plant harvested by man, but there are often correlated effects on other parts of the plant, producing an overall gigas effect similar to that seen in some polyploids. However, in diploid cultigens, this occurs without any increase in chromosome number or DNA content. Chile peppers are all diploid, but domesticated peppers not only have larger fruits than wild peppers but also have larger leaves, flowers and seeds. An overall increase in size of many different organs could result from an increase in cell number, cell size or both. In tomato, pericarps and placentas of fruits of near-isogenic lines with small vs. large fruits contain cells of similar size but there are more cells in the large fruits (Cong *et al.*, 2002). There are also more carpels, and this is often associated with an increase in the numbers of other floral parts. The number of floral parts in tomato is determined by the size of the floral meristem, which in turn depends on the number of cells in the L3 layer of the shoot apical meristem (Grandillo *et al.*, 1999), showing that the increase in cell number in large-fruited domesticated tomatoes is not confined to the fruit.

Increased morphological variability

This also is especially marked in the part of the plant used by man. Domesticated chile peppers and tomatoes vary in fruit shape and colour, as well as size; domesticated potatoes vary in shape of the tuber and colour of both skin and flesh; domesticated beans have testas of various colours and patterns. Such variation may act as a marker for variation in less visible characters affecting the way in which the crop is used. In Amazonia, chile fruits of a particular colour and shape are said to be the best for seasoning turtle, while others, of different colour and shape, are known as perfume peppers because they have a good aroma as well as pungency.

Boster (1985) called this selection for perceptual distinctiveness, and cited cassava as an example. Cassava is propagated by stem cuttings. Vegetative traits are therefore the only features by which cultivators can identify different variants of cassava at planting or before harvest. The different types of cassava grown by the Aguaruna Jívaro of upper Amazonia display a great range of morphological variation in the inedible stems and leaves, and Boster (1985) attributed this to selection for perceptual distinctiveness.

Changes in plant habit

The type of germination does not usually vary within species, but Pujol *et al.* (2005) found that cassava (*Manihot esculenta* ssp. *esculenta*) has epigeal germination whereas its immediate wild progenitor (*M. esculenta* ssp. *flabellifolia*), together with other closely related wild species, has hypogeal germination. These wild taxa are all found in savanna vegetation subject to periodic fires. Hypogeal seedlings can regenerate from buds in the axils of the cotyledons and cataphylls, because these survive underground when above-ground parts are burned. The epigeal seedlings of the domesticate have aerial photosynthetic cotyledons that promote rapid early growth, which is adaptive under conditions of slash-and-burn agriculture. Volunteer seedlings of cassava are tolerated and evaluated, although the crop is usually propagated vegetatively (Salick *et al.*, 1997; Elias and McKey, 2000). The unusual polymorphism for germination within *M. esculenta* may thus have arisen through disruptive selection in the agricultural vs. natural environments.

Selection for increased harvest index (ratio of harvested to total biomass produced) may result in reduced or suppressed lateral branching (Evans, 1993). Modern single-headed sunflowers are an extreme example, but grain chenopods similarly have a larger, more compact terminal inflorescence and fewer lateral inflorescences than their weedy relatives (Wilson and Heiser, 1979). In cereals, including maize, some of the basal tiller shoots are often suppressed, reducing the number of inflorescences per plant and producing more synchronous ripening of grain on an individual plant and within a stand, facilitating harvesting of the stand as a whole.

Greater synchronization of maturity is also favoured by a determinate habit, either of inflorescence branches, as in determinate variants of *Amaranthus caudatus* (Kulakow,

1987), or of vegetative branches, as in some types of bush bean (Smartt, 1969). All types of bush bean have fewer nodes and shorter internodes than climbing beans (Smartt, 1969), so are self-supporting. Bush types of squash similarly have much shorter internodes than trailing types (Whitaker and Davis, 1962).

Loss of seed dormancy

Rapid uniform germination is necessary if a stand of a crop is to be established before there is serious competition from weeds and if plants in the stand are to mature at the same time. Seed dormancy is often associated with the presence of germination inhibitors in the testa and/or impermeability of the seed to water. In *Chenopodium*, the outer layer of the testa, responsible for the black colour of seeds of wild and weedy forms, is reduced or absent in domesticates, whose seeds are therefore usually pale in colour (Wilson, 1981; Bruno, 2006). Seeds of many wild legumes have thick testas and may become increasingly impermeable to water on drying (Lush and Evans, 1980). These features are disadvantageous in domesticates, not only because such seeds germinate slowly but also because they may require prolonged soaking and removal of some of the seed coats before they can be cooked (Lush and Evans, 1980). Domesticated grain legumes therefore generally have thinner testas than their wild progenitors.

Loss of chemical or mechanical protection

Many domesticates have completely or partially lost the secondary metabolites that protect their wild relatives against herbivores. Tubers of wild potatoes contain bitter glycoalkaloids at levels that may be toxic to humans (Johns, 1989); domesticated potatoes do not. Bitter cassava contains a cyanogenic glycoside throughout the tuberous root that has to be removed by various methods of post-harvest processing; whereas in sweet cassava toxic levels of glycoside are confined to the outer layers of the root, so are removed simply by peeling (Purseglove, 1968). Fruits of wild species of *Cucurbita* contain bitter cucurbitacins; fruits of the domesticated species used as vegetables or containers for liquids do not. However, domesticated tobacco (*Nicotiana tabacum*) contains nicotine, valued by man for its narcotic properties and as an insecticide, in both green and dried leaves, but in wild species nicotine is demethylated to nornicotine (Gerstel, 1976), whose role in chemical protection is not reported.

Other species, mechanically protected by spines, have become spineless through human selection. Salick (1992) has demonstrated that there is strong selection by farmers against spines in cultivated cocona (*Solanum sessiliflorum*) and strong selection for spines in wild plants. Some domesticated types of the peach palm (*Bactris gasipaes*) have similarly lost the spines from their trunks (Balick, 1984).

Photoperiodism

Diamond (2002) pointed out that in the Americas the spread of agriculture was mostly across latitudes. Crops

consequently needed to adapt to different daylengths, which Diamond suggested would result in domesticates spreading more slowly in the Americas than in Europe or Asia. However, when selection pressures are strong, changes in daylength reaction may evolve relatively rapidly. The first potatoes to reach Europe produced tubers only in short days, but 200 years later clones adapted to long days had developed (Simmonds, 1976).

GENETIC CONTROL OF TRAITS OF THE DOMESTICATION SYNDROME

Studies based on Mendelian genetics

Until recently, the genetic control of features distinguishing domesticated plants from their wild relatives had to be investigated by the classic Mendelian technique of crossing parents with different phenotypes and analysing ratios in the segregating progeny. Many of the qualitative changes associated with domestication were thereby found to be controlled by one or a few major genes, for example loss of seed dispersal and change to determinate habit in domesticated common bean (Koinange *et al.*, 1996), loss of fruit dispersal and loss of pungency in domesticated *Capsicum* peppers (Lippert *et al.*, 1966), loss of bitter cucurbitacins in the domesticated squashes (Whitaker and Davis, 1962), presence of pale seed in the grain amaranths (Kulakow *et al.*, 1985) and inactivation of the enzyme that converts nicotine to normicotine in wild species of tobacco (Gerstel, 1976).

Quantitative characters, such as differences in size or shape, show continuous variation in segregating progeny, so were considered to be controlled by many genes with individually small effects (polygenes). However, the distinction between qualitative and quantitative characters, with oligogenic or polygenic control, is not entirely clear-cut. For example, whether the fruit separates from the receptacle in *Capsicum* depends in part on how hard one pulls, pungent peppers vary in the degree of pungency, and Gerstel (1976) reported that the two wild progenitors of allotetraploid *N. tabacum* differ in activity of the enzyme that converts nicotine to normicotine and how late in the life of the leaf it acts. Many qualitative characters are therefore now thought to be controlled by one or a few major genes plus modifiers which dilute or alter the expression of the major gene(s). Conversely, for many quantitative characters a small number of loci have been found to have large effects, so may be studied as segregating Mendelian factors, while other loci affecting the same character have lesser effects, so are not amenable to Mendelian analysis.

DNA markers and the study of quantitative trait loci

A major advance in the study of the genetics of domestication came with the development of DNA markers, which made it possible to produce saturated linkage maps for many crops and then to determine, by looking for associations with these markers, how many and which regions of the genome carry factors affecting a given

quantitative trait (quantitative trait loci or QTLs). In this way, 28 different QTLs affecting fruit weight in tomato have been located, though alleles at just one of these (*fw2-2*) account for about 30% of the difference between large- and small-fruited tomatoes (Cong *et al.*, 2002). Koinange *et al.* (1996) found that four QTLs explained 69% of the phenotypic variation in seed dormancy in domesticated vs. wild common bean, four other QTLs explained 57% of the variation in seed weight and three QTLs explained 37% of the variation in pod length. Similar studies have now been conducted on enough different crops to suggest that QTLs with large effects (accounting for >25% of the phenotypic variation) have frequently been selected during domestication and that differences between domesticate and wild progenitor are often controlled by only 2–5 QTLs per trait (Gepts, 2004). Sunflower is an exception, in that of 78 QTLs found to affect traits involved in domestication, only four (affecting four different traits) are large-effect QTLs (Burke *et al.*, 2002).

Poncet *et al.* (2004) argued that the early stages of domestication probably involved fixation of alleles at QTLs with major effects, while subsequent improvements involved accumulation of changes at loci with minor effects. American wild rice (*Z. palustris*) is a crop that has recently crossed the threshold from exploitation to domestication. Early studies (Hayes *et al.*, 1989) suggested that two loci control shattering, but Kennard *et al.* (2002) found three loci, one with a major effect and two with much smaller effects. They suggested that, during the years separating these two studies, a non-shattering allele at a third locus could have been selected. Nesbitt and Tanksley (2002) considered that fixation of the large-fruit allele at *fw2-2* in domesticated tomatoes was followed by stacking of large-fruit alleles at many of the other QTLs shown to affect fruit size in tomato. If such stacking of favourable alleles is indeed an ongoing process during domestication, then it is not surprising that in crops that have been subjected to human selection for long periods, traits of the domestication syndrome should each be controlled by multiple loci.

If domestication depended on *de novo* occurrence and selection of mutants in crop populations grown by early farmers, then improvement would probably have proceeded slowly, limited by the mutation rate and the ability of early farmers to detect and propagate favourable phenotypes. Conventional wisdom is that characters favoured by human selection, such as increased size or loss of dispersal, are disadvantageous or even lethal in the wild. However, there are increasing numbers of reports of 'domesticated alleles' in extant populations of wild progenitors of crops. In *Z. palustris*, the non-shattering trait was found in a paddy planted with wild-type seed (Hayes *et al.*, 1989). Burke *et al.* (2002) reported that alleles at a number of QTLs in the wild sunflower used as parent of their mapping population produce a phenotype like the domesticated parent, so argued that sunflower may have been readily domesticated. Nesbitt and Tanksley (2002) found that most accessions of cherry tomato (the progenitor of the domesticated tomato) carry the allele for large fruit at *fw2-2*. The 'maize' allele of the gene *teosinte branched1*

(*tb1*), which produces a maize-like female inflorescence in the background genotype of maize, occurs with a frequency of >30% in teosinte, the closest wild relative of maize (Jaenicke-Després *et al.*, 2003). Seeds with thin testas are present in low frequency in wild *C. berlandieri* in eastern North America, though Gremillion (1993) does not make clear whether the polymorphism is between plants within a population or between different seeds on the same plant. Within-plant polymorphism for testa characters affecting germination is well known in the closely related *C. album*, where the ratio of the different morphs may be environmentally controlled (Harper, 1977). Although it may seem difficult to fix such a character by human selection, Lukens and Doebley (1999) suggested that domestication of maize may have involved selection for allele(s) with reduced environmental plasticity, and cited a model suggesting that morphological evolution may occur rapidly when selection favours one morph of a phenotypically plastic species.

It is hard to discount completely the possibility that 'domesticated alleles' in wild populations result from gene flow from the crop, but their survival and frequency suggest that these alleles are less deleterious in the wild than previously thought. This is possibly because their expression in the background genotypes of wild plants is less extreme than in the genotypes of domesticates modified by human selection which has probably also affected other loci influencing the same trait. Nesbitt and Tanksley (2002) were unable to tell from the size of the fruits which accessions of cherry tomato carry the large-fruit allele of *fw2.2* and which do not, and the effect of the 'maize' allele of *tb1* in the genetic background of teosinte is not clearly established (Clark *et al.*, 2004). The mutation rate may therefore have been less of a constraint on domestication than the ability of early farmers to detect and fix favourable phenotypes.

Orthologies of genes involved in domestication

The markers used to construct a saturated linkage map of one species may be used to construct linkage maps for other crops in the same family. By this means, it has been possible to compare the position of QTLs involved in the domestication syndrome in maize, sorghum and rice (Paterson *et al.*, 1995), and in aubergine, tomato and chile pepper (Doganlar *et al.*, 2002). In both groups, QTLs controlling similar traits map to the same conserved regions of the genome, suggesting that changes at the same loci were selected during domestication. However, Le Thierry d'Ennequin *et al.* (1999) noted that QTLs associated with convergent domestication in cereals actually account for <50% of the phenotypic variance, so selection at different loci in these crops may have been at least as influential as convergent change in achieving the domesticated phenotype. Paterson (2002) additionally cautioned that the presence of QTLs affecting the same trait in the same position in the genome does not prove that the underlying genes are in fact identical. Ben Chaim *et al.* (2001) identified three QTLs affecting fruit shape in *Capsicum* that they suggested are orthologous to fruit shape QTLs in

tomato. However, fruit shape in tomato is basically determined before flowering, whereas in *Capsicum* differences in fruit shape arise after flowering (Grandillo *et al.*, 1999). This suggests that either the genes, or the regulation of the genes, at these putatively orthologous loci are different.

Sequencing studies and the action of genes involved in domestication

Once the candidate gene associated with a particular trait has been isolated, alleles governing different phenotypes can be sequenced. In this way, several presence-or-absence qualitative characters have been shown to be controlled by changes affecting the functioning of the gene product. Yellow fruits are recessive to red in *Capsicum*. They lack the red pigments capsanthin and capsorubin, whose formation is catalysed by the enzyme capsanthin-capsorubin synthase (CCS). In *C. annuum*, yellow-fruited plants are homozygous for a deletion at the 5' end of the coding region of the gene encoding CCS (Lefebvre *et al.*, 1998; Popovsky and Paran, 2000) so do not produce a functional enzyme. In maize, *sugary1* encodes one of the enzymes responsible for converting sugar to the amylopectin fraction of starch (Whitt *et al.*, 2002). Sweet corns are homozygous recessive and carry sequence changes that either disrupt translation of the gene or change a conserved residue in the gene product (Whitt *et al.*, 2002). Sequencing of the wild-type *JOINTLESS* allele of tomato showed that its protein product belongs to the MADS-box family of transcription factors (Mao *et al.*, 2000), which are involved in determining sites of cell differentiation (Roberts *et al.*, 2002). The *jointless* allele, which causes loss of the abscission zone in the pedicel, carries a deletion for the whole of the first exon of this gene (Mao *et al.*, 2000).

There are as yet relatively few studies on the mode of action of genes responsible for quantitative traits. Cong *et al.* (2002) studied the QTL *fw2.2* responsible for much of the variation in fruit weight in tomato and found that the large-fruit allele is associated with longer periods of cell division in pericarp and placenta, explaining the observed increase in cell number. They found that the large-fruit allele is transcribed more rapidly than the small-fruit allele and that the timing of transcription is inversely correlated with mitotic indices in pericarp and placenta, suggesting that *fw2.2* is a negative regulator of cell division. Sequencing studies indicated no apparent functional differences in the proteins produced by large-fruit or small-fruit alleles, but the upstream promoter region of the large-fruit allele showed eight unique changes. Much of the difference between large and small fruit was therefore attributed to differences in expression of *fw2.2* (Nesbitt and Tanksley, 2002).

In maize, the nucleotide sequence of the gene *tb1*, which affects the number of tillers at the base of the plant as well as the morphology of the lateral branches, suggests that it belongs to the TCP family of genes that regulate transcription and that it represses growth of organs in which its mRNA accumulates (Doebley, 2004). There are no fixed differences between maize and teosinte in the predicted

amino acid sequences of the protein product of *tb1*, or in 1.1 kb of the non-transcribed region upstream of the *tb1* transcriptional unit (Wang *et al.*, 1999). However, nucleotide diversity is strongly reduced upstream of the transcriptional unit, including the part of the non-transcribed region where sequences regulating gene transcription are typically found, suggesting that this region has been the target of strong selection and that changes in the regulation of *tb1* rather than in the product encoded by *tb1* underlie the morphological differences associated with *tb1* (Wang *et al.*, 1999; Doebley, 2004).

A second QTL important in controlling differences in the female inflorescence in *Zea* is *teosinte glume architecture 1* (*tg1*). This QTL controls the depth of the cavity or cupule that encloses the grain of teosinte, the three-dimensional growth of the glume that closes the entrance to the cupule in teosinte, and induration and silicification of the glume and rachis segments in teosinte. These multiple effects suggested to Wang *et al.* (2005) that *tg1* is a regulatory gene at the head of a developmental cascade. Sequencing of *tg1* showed that it is homologous to squamosa-promoter-binding protein transcriptional regulators and that a fixed difference between the *tg1* sequences of teosinte and maize leads to substitution in maize of one amino acid at what appears to be a crucial position for function or stability of the protein product of *tg1* (Wang *et al.*, 2005). Nucleotide diversity is markedly reduced in the promoter region and exon 1 of *tg1*, but not in exons 2 and 3, indicating that *tg1* has been exposed to strong selection but, as in *tb1*, this has affected only part of the gene.

Vigouroux *et al.* (2002) used similar reductions in diversity, but of microsatellites rather than nucleotides, to screen 501 maize genes for evidence of selection during domestication. They found 15 candidate genes, only six of which have any homology with genes of known function. Four of these six show homology to various transcription factors (Vigouroux *et al.*, 2002).

These studies on gene action and the genes that have apparently been targets of selection during domestication have suggested to some workers, e.g. Doebley *et al.* (2006), that changes in gene regulation rather than changes in gene function account for the most important changes in plant domestication.

MULTIPLE DOMESTICATION AND MULTIPLE ORIGINS OF DOMESTICATION TRAITS

A feature of crop domestication in the Americas is the number of examples of independent domestication of different species in the same genus, or occasionally of the same species (Table 2). New World crops are therefore potentially useful resources for investigating the still-unresolved question of whether similar changes have been selected independently, resulting in parallel or convergent evolution of the domestication syndrome, or whether different mutations have been selected in different regions, so that similar phenotypes are actually controlled by different genotypes.

Prior to the advent of molecular genetics, this question could be addressed only by crossing the related

domesticates. If the F₁ shows the wild-type phenotype, then the two domesticates are assumed to carry mutations at different, complementary, loci and thus to have evolved the trait in question independently. Cheng (1989) crossed a non-pungent bell pepper (*Capsicum annuum*) with a non-pungent accession of the closely related *C. chinense*, and found that the F₁ had extremely pungent fruit. This suggests that the pathway to synthesis of the pungent principle, capsaicin, is blocked at a different point in each species and that different mutations to non-pungency have been selected in what are regarded, on morphological and cytological grounds, as independently domesticated taxa (Pickersgill *et al.*, 1979). Similarly, when the South American domesticate *Chenopodium quinoa*, which has pale seeds, was crossed with a pale-seeded accession of the Mesoamerican domesticate *C. berlandieri* ssp. *nuttalliae*, the F₁ had black seeds (Heiser and Nelson, 1979), so pale seeds are presumably controlled by mutations in different genes in the two species, supporting the view that each was domesticated independently.

Studies on crosses between the domesticated species of *Cucurbita* have given somewhat ambiguous results. Bush vs. wild-type vine habit has been reported to be controlled by a single gene, probably the same gene, in *C. pepo* and *C. maxima* (Robinson *et al.*, 1976). Whitaker (1951) showed that the hard rind of wild *C. andreana* is dominant to the soft rind of domesticated *C. maxima* and controlled by a single gene. Pearson *et al.* (1951) crossed cultivars of *C. moschata* and *C. maxima* with soft rinds and found that fruits of the F₁ had hard rinds when the cross was made in one direction, but soft rinds in the reciprocal cross. On the other hand, when Piperno *et al.* (2002) crossed the more closely related *C. argyrosperma* and *C. moschata*, again using cultivars with soft rinds as parents, fruits of the F₁ and F₂ all had soft rind. Borchers and Taylor (1988) found that the F₁ hybrid between non-bitter cultivars of *C. argyrosperma* and *C. pepo* had bitter fruit and carried dominant alleles at three loci governing synthesis of cucurbitacins. The *C. pepo* parent was homozygous recessive at one of these loci and the *C. argyrosperma* parent was homozygous recessive at the other two, so synthesis of cucurbitacins was blocked at different points in the two species, implying that non-bitterness had been selected independently in each species. These various studies therefore suggest that for some elements of the domestication syndrome the same phenotype has a different genetic basis in different domesticates, but for other traits human selection under domestication may have favoured independently occurring mutations in the same gene.

In grain amaranths, crosses between pale-seeded forms of the two Mesoamerican domesticates, *A. cruentus* and *A. hypochondriacus*, and between *A. hypochondriacus* and Andean *A. caudatus*, produced only pale-seeded F₁s (Kulakow *et al.*, 1985). Kulakow *et al.* (1985) argued from this that pale seed evolved only once, supporting the hypothesis that grain amaranths were domesticated only once in the Americas and the three species differentiated after domestication. Against this is the finding of Hauptli and Jain (1978) that different traits are correlated with yield in the different domesticates. In *A. hypochondriacus*,

TABLE 2. Genera in which two or more species have been domesticated in the Americas and regions of domestication of the relevant species

Family/genus	Eastern North America	Mesoamerica	Andean region	Tropical lowland South America	Comments
Amaranthaceae <i>Amaranthus</i>		<i>A. cruentus</i> <i>A. hypochondriacus</i>	<i>A. caudatus</i>		Still unclear whether there was more than one domestication from distinct wild progenitors or whether a single domestication was followed by speciation
Chenopodiaceae <i>Chenopodium</i>	<i>C. berlandieri</i> ssp. <i>jonesianum</i>	<i>C. berlandieri</i> ssp. <i>nuttalliae</i>	<i>C. quinoa</i> <i>C. pallidicaule</i>		Not yet conclusively established that <i>C. berlandieri</i> was domesticated independently in North America and Mesoamerica
Cucurbitaceae <i>Cucurbita</i>	<i>C. pepo</i> ssp. <i>ovifera</i>	<i>C. pepo</i> ssp. <i>pepo</i> <i>C. argyrosperma</i> <i>C. moschata</i>	<i>C. ficifolia</i> <i>C. maxima</i> <i>C. moschata</i>		Ancestry of <i>C. moschata</i> and hence whether it was domesticated more than once still uncertain
Fabaceae <i>Arachis</i>			<i>A. hypogaea</i> <i>A. villosulcarpa</i> <i>C. plagiosperma</i>		
<i>Canavalia</i>		<i>C. ensiformis</i>			<i>C. ensiformis</i> and <i>C. plagiosperma</i> are reported to produce fertile hybrids, so their status as distinct species and possible independent domestication need reinvestigation
<i>Pachyrhizus</i>		<i>P. erosus</i>	<i>P. ahipa</i>	<i>P. tuberosus</i>	<i>P. erosus</i> and <i>P. tuberosus</i> may be conspecific, hence possibly not independently domesticated. The wild progenitor of <i>P. ahipa</i> is not known.
<i>Phaseolus</i>		<i>P. vulgaris</i> <i>P. lunatus</i> <i>P. coccineus</i> <i>P. acutifolius</i> <i>P. dumosus</i>	<i>P. vulgaris</i> <i>P. lunatus</i>		
Malvaceae <i>Gossypium</i>		<i>G. hirsutum</i>	<i>G. barbadense</i>		
Solanaceae <i>Capsicum</i>		<i>C. annuum</i> <i>C. frutescens</i>	<i>C. baccatum</i> <i>C. pubescens</i>	<i>C. chinense</i>	
<i>Nicotiana</i>			<i>N. rustica</i> <i>N. tabacum</i> <i>P. peruviana</i>		
<i>Physalis</i>		<i>P. philadelphica</i>			
<i>Solanum</i>			<i>S. muricatum</i> <i>S. quitoense</i> <i>S. tuberosum</i>	<i>S. sessiliflorum</i>	
Sect. <i>Basarthrum</i>					
Sect. <i>Lasiocarpa</i>					
Sect. <i>Petota</i>					

seed yield correlates with length of the inflorescence, and the number of female flowers per flower cluster is relatively constant, while in *A. cruentus* and *A. caudatus* seed yield is not correlated with length of inflorescence but with the number of female flowers per cluster. This suggests that selection for increased yield has proceeded independently in the different domesticates.

The study of complementation between alleles controlling similar traits in different species depends on the ability to cross domesticates belonging to different species. Barriers to crossing and sterility of interspecific hybrids often impose severe limitations on such studies. The data may also be equivocal because gene expression may change in hybrid genotypes. Comparative studies of the molecular basis of single-gene mutants selected under domestication may therefore be more informative with regard to multiple origins of traits of the domestication syndrome. It is difficult to obtain interspecific hybrids between domesticated accessions in *Capsicum* (Pickersgill, 1971), so it has not been possible to determine whether the homologous series of variants in fruit colour represent the same mutations in the same genes in each domesticate. Now, however, it would be relatively easy to amplify the gene coding for CCS from yellow-fruited accessions of each domesticate and determine whether the deletion present in *C. annuum* is responsible for yellow fruit in the other domesticated species. Similarly, the gene coding for capsaicin synthase, the enzyme that catalyses the final step in the synthesis of capsaicin, has recently been identified (Prasad *et al.*, 2006), so it should be possible to compare sequences for this gene from pungent vs. non-pungent accessions of the different domesticated species.

Sequencing studies may also constitute a useful tool for investigating possible multiple origins and spread of particular variants within a crop. Mangelsdorf (1974) considered that the sweet corns of Middle and North America were all derived from a single Peruvian race. All are homozygous recessive *su1 su1*, but Whitt *et al.* (2002) have shown that North American sweet corns carry a nucleotide substitution resulting in a single amino acid change in the gene product, whereas in Mexican sweet corns a transposable element has inserted into exon 1 of *su1*. The 'sweet' mutation has therefore arisen independently at least twice and the sweet corns of North America and Mexico cannot both result from northward spread of a South American sweet corn. This example suggests caution in accepting apparent homology of the pale-seeded mutation in the different species of grain amaranth as evidence for a single domestication. If different changes have occurred in the nucleotide sequence of the gene responsible for pale seeds in the different species, then lack of complementation in the F_1 of a cross between two pale-seeded species does not prove identity of the underlying mutations even though the mutations are in the same gene.

PAST DOMESTICATION AS A GUIDE TO FUTURE IMPROVEMENT OF NEW WORLD CROPS

The developing understanding of the genetic control of various traits of the domestication syndrome and of the mode of action of some of the genes involved may assist

in realizing the potential of some of the minor domesticates of the New World. Crops such as goldenberry (*Physalis peruviana*), pepino (*Solanum muricatum*) and yam bean (*Pachyrhizus erosus*) command high prices in markets in some developed countries (National Research Council, 1989), so are potentially useful export-earners for the developing countries in which they originated. Naranjilla (*Solanum quitoense*) and cupuaçu (*Theobroma grandiflorum*) have attracted the attention of commercial companies in developed countries, but problems of reliably producing large quantities of fruit have led to loss of potentially valuable export markets (National Research Council, 1989; Smith *et al.*, 1992). These and other lesser known domesticates need further improvement to adapt them to a wider range of environments, modify their morphology for mechanized monoculture and/or increase pest and disease resistance. Conventional plant breeding programmes require expensive investment in time, labour and land, and neither commercial companies nor governments of developing countries have given much support to such programmes for the minor crops. Application of information from molecular genetics could accelerate improvement of at least some of these crops.

The most rapid benefits may come from the increasing numbers of saturated linkage maps and of DNA sequences in databanks. Thus, Kennard *et al.* (2002) used markers previously mapped in Asiatic rice (*Oryza sativa*) to construct a genetic map for American wild rice (*Zizania palustris*), and noted that breeding of wild rice is now poised to benefit from the mapping of comparative traits in the two crops. *Capsicum annuum* is poorly adapted to the hot humid conditions of the lowland tropics, where it is replaced by *C. chinense*. Non-pungent forms of *C. chinense* exist but have encountered problems of acceptance among consumers accustomed to bell pepper (*C. annuum*) because fruits of non-pungent *C. chinense* are smaller and more irregular in shape than bell pepper (Cheng, 1989). Comparative maps are now available for *Solanum*, *Lycopersicon* and *Capsicum* (Doganlar *et al.*, 2002), so it may be possible to exploit the genetic diversity available for fruit characters within *C. chinense* by identifying QTLs orthologous with those affecting fruit size or shape in tomato, then using marker-assisted selection to stack favourable alleles for large 'blocky' fruit, reproducing in a short time what may have taken centuries of human selection in bell pepper.

Modifications of plant habit often result in increased harvest index or permit denser planting, thereby increasing yield per unit area. The bush habit may be desirable in climbing legumes or trailing cucurbits when these are grown in monoculture. However, bush types occur in only one or two of the domesticated species of *Phaseolus*, *Pachyrhizus* and *Cucurbita*. In bush types of both *Phaseolus* and *Cucurbita*, internodes are much shorter than in vine types. Peng *et al.* (1999) showed that the dwarfing genes *Rht-B1* and *Rht-D1* in wheat and *d8* in maize are functional orthologues of *gai* in *Arabidopsis*, which has similar effects to the cereal genes on both plant height and response to gibberellin. They produced a transgenic basmati rice expressing the *gai* protein, found that it was dwarfed compared with controls without the transgene, and concluded that it is now possible to

insert the genetically dominant dwarfing allele of the *gai* gene into any crop that can be transformed. This obviates the need for lengthy conventional breeding programmes and carries minimal risk of disrupting pre-established commercially or agronomically desirable genotypes. It would be interesting to investigate whether the bush genes of *Phaseolus* and *Cucurbita* are also functional orthologues of *gai*, and whether it is feasible and/or desirable to develop bush types in crops such as lima bean, yam bean, *C. moschata* and the minor cucurbits chayote (*Sechium edule*) and caihua (*Cyclanthera pedata*).

The discovery of intraspecific polymorphism for hypogeal vs. epigeal germination in cassava (Pujol *et al.*, 2005) opens the way to investigation of its genetic control and the mode of action of the controlling genes. This might then permit a search for orthologous genes in, for example, *Phaseolus*. Bean breeders have attempted, so far unsuccessfully, to improve cold tolerance of epigeal *P. vulgaris* by transferring hypogeal germination from *P. coccineus*, assuming that this would enable regeneration from underground buds if above-ground parts of *P. vulgaris* seedlings were killed by frost (Sullivan, 1988).

In grain amaranths, the dehiscent fruit allows easy threshing and winnowing by traditional methods, but results in significant seed loss when the crop is harvested mechanically (National Academy of Sciences, 1975). Understanding the genetic control and mode of action of genes involved in abscission could pave the way for development of an indehiscent grain amaranth, though this may pose further problems in threshing the crop with existing machinery.

Eventually it may even be possible to expand the environmental adaptation of crops such as pepino and naranjilla, both currently confined to a very narrow range of environments (National Research Council, 1989; Prohens *et al.*, 1996). Vigouroux *et al.* (2002) suggested that their technique for identifying unknown genes of agronomic importance that have been targets of human selection during maize domestication could be adapted to locate and then identify other unknown genes subjected to similar selective sweeps during adaptation to environmental stresses such as drought or heat and humidity. Once such genes have been identified in maize, a search could be made for their orthologues in other crops. Cocona, adapted to Amazonia, has been crossed with naranjilla, which is confined to highland Latin America, and the hybrids are extensively grown in Ecuador (Heiser and Anderson, 1999). Although these hybrids are not reported to tolerate a wider range of growing conditions than 'pure' naranjilla, cocona is a possible source of QTLs for adapting naranjilla to high temperatures.

It remains to be seen which suggestions for exploiting studies on the molecular genetics of plant domestication are practically feasible. Understanding the molecular basis of evolution under human selection is still at an early stage and the best is surely yet to come.

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