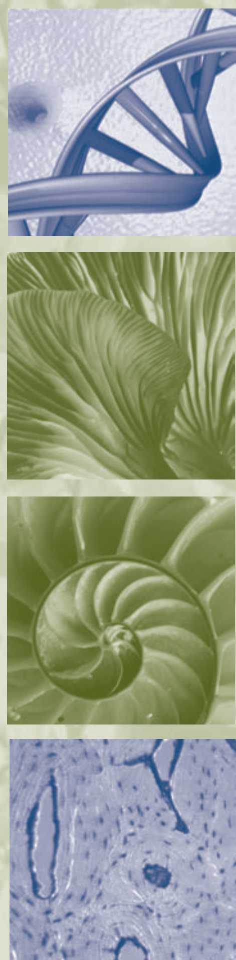

Part 5

Evolutionary Science: Advancing Societal Well-Being

Chapter 16

Plant and Animal Domestication as Human-Made Evolution

Paul Gepts

> No doubt man selects varying individuals, sows their seeds, and again selects their varying offspring. . . . Man therefore may be said to have been trying an experiment on a gigantic scale; and it is an experiment which nature during the long lapse of time has incessantly tried.
> — Charles Darwin, 1868

Introduction

When Charles Darwin published the *Origin of Species* in 1859, he was faced with a conundrum, namely, that "the laws governing inheritance are quite unknown; no one can say why the same peculiarity in different individuals of the same species, and in individuals of different species, is sometimes inherited and sometimes not so; why the child often reverts in certain characters to its grandfather or grandmother or other much more remote ancestor; why a peculiarity is often transmitted from one sex to both sexes or to one sex alone, more commonly but not exclusively to the like sex."

Whereas Gregor Mendel would publish the results of his experiments a few years hence (in 1866), his results would remain unacknowledged until the beginning of the 20th century. The role of chromosomes in heredity and the phenomena of mitosis and meiosis were discovered only toward the end of the 19th, beginning of the 20th century. The role of DNA as the biochemical vehicle of heredity was only conclusively established in the 1940s. Thus, while heredity was well accepted, its mechanism remained uncertain for quite some time after 1859. Yet heredity played an all-important role in Darwin's theory because it assured that the progeny of the fittest individuals would themselves be fitter than the progeny of less fit individuals. Thus, heredity potentially introduces a multiplier effect that strengthens the effect of selection.

In the face of this situation, Darwin chose to document the cumulative effects selection can have generation after generation by examining the domestication of plants and animals by humans. In addition to the first chapter of the *Origin of Species,* which is devoted to domestication, he also published a later book, *The Variation of Animals and Plants under Domestication* (1868), about this topic. His focus on human selection may be somewhat paradoxical, as the *Origin of Species* is focused on natural selection, but the same evolutionary processes are at work in natural and artificial selection, although the magnitude of these factors may differ. For example, one can speculate that selection to achieve and maintain the domesticated (and wild) phenotypes may be quite strong given the contrasts between wild and domesticated environments and the short time span for domestication to take place.

The Process of Domestication

Domestication can be defined as a selection process leading to the adaptation of plants and animals to cultivation or rearing by humans. Agriculture started some 10,000 years ago when the first farmers started cultivating plants or rearing animals in captivity, which up to then they had gathered or hunted. Through cultivation or captivity rearing, humans imposed several selection pressures, chief among them a control over reproduction of the plants or animals.

The traits selected during domestication differ between plants and animals. In the former, they are primarily morphological and physiological. In the latter, they are primarily behavioral and to a lesser extent morphological. Because plant or animal populations are generally heterogeneous, the cultivation or rearing process exerts selection pressure on natural mutants that exist within these populations. Although these mutants occur generally at a low frequency initially (in part because of the low frequency of mutations and in part because of the condition of a deleterious phenotype in the wild), repeated positive selection in successive generations in a cultivated environment may gradually increase their frequency until the mutation achieves fixation, that is, it is present in all individuals of the cultivated population (Hillman & Davies, 1999).

An example of such a mutation is a seed dispersal mutant. In natural populations, plants disperse their seeds without human intervention at maturity of the fruit or the plant. This trait is obviously essential for the wild plant to thrive in wild environments. Mutants that prevent seed dispersal may appear in such populations but their fitness is very low. Their frequency will, therefore, remain low. If these populations are now subjected to cultivation, the same mutation will now potentially be favored because—at least for some harvest methods—they prevent loss of seeds during and after harvest.

Selection during domestication may encompass both natural and human selection. To what extent human selection was conscious or unconscious in the first stages of domestication is still a matter of conjecture. Most scientists involved in this type of study think the first stages of domestication were probably the result of unconscious selection on the part of humans. However, in later stages, humans took probably a more active role in selecting traits they liked either because they made farming easier or more beneficial or because they made the products more useful, attractive, or palatable.

Cultivation or rearing by themselves is only a necessary but not sufficient condition for domestication. The sufficient condition requires heritable genetic changes, which translate into markedly distinct morphological and physiological phenotypes. *Fully* domesticated organisms such as maize (*Zea mays*) cannot survive in the wild without human intervention, emphasizing the distinctness between wild and domesticated types. Therefore, as long as cultivation or rearing does not bring about significant genetic changes, domestication has not been initiated. Conversely, humans have come to rely on domesticated plants and animals for a significant part of their food (and other needs, as well). Hence, one can speak of a mutually beneficial relationship between humans and their crops or animal breeds, in which both sides need the other for survival.

Selection and mutation are not the only evolutionary factors that have played an important role during domestication. Whereas selection and mutation affect specific loci, both random drift and migration affect the genome as a whole. Random drift, because of sampling effects caused by small population size, has affected crop plants and farm animals repeatedly during and after domestication. It is becoming increasingly apparent from molecular studies that domestication has taken place in a specific region in most crops and domestic animals. Thus, the initial population sizes were probably small, which led to genetic bottlenecks with the attending random drift. Further genetic bottlenecks were encountered during crop failures and dispersal of crops or breeds from their original domestication areas.

Traits Selected under Domestication

To further illustrate the selection process that took place during domestication, it is useful to review more systematically the traits that were selected. Domestication, in general, leads to heritable morphological, physiological, genetic, and behavioral changes. In both plants and animals, the number of species that were actually domesticated compared with the total number of species is very small. In animals, in particular, this observation has led scientists to suggest that there is a preadaptation for domestication (table 1; Price, 2002). This wide range of traits may explain why few vertebrate animals have been domesticated. Of some 5,000 species (Myers, 1999), fewer than 20 have been domesticated (Clutton-Brock, 1999), mostly among ungulates and gallinaceous birds. However, this does not mean that other animals could not be domesticated. For example, starting in 1959, silver foxes were selected in the former Soviet Union for their nonaggressive and doglike behavior toward humans (Belyaev, 1979; Trut, 1999). Cameron-Beaumont, Lowe, & Bradshaw (2002) pointed out that in the cat family small felids other than the domestic cat display affiliative or affectionate behavior toward humans, for example, in the ocelot lineage of South America, which has never been

Category	Pre-adaptation
Social structure of populations	Large, gregarious social groups (including males and females) with dominance hierarchy
Intra- and interspecies behavior	Nonaggressiveness
Response to humans	Short flight distance, nonaggressiveness
Sexual behavior	Promiscuous mating
Parental behavior	Young easily separated from parents
Environmental adaptation	Limited sensitivity to changes in environment
Locomotor activity	Limited agility; small home range
Feeding behavior	Generalized feeder or omnivorous

***Source*: Modified from Price, 2002.**

Table 1. Some preadaptations of vertebrate animals to domestication.

domesticated. They concluded that ecological and geographic separation between humans and potential domesticates could explain why only some species were domesticated.

There are some 250,000 angiosperm species. Of those, fewer than 500 have been subject to at least some attempts at domestication (Harlan, 1992). Morphological traits distinguishing domesticated plants from their wild ancestors have resulted from selection at various developmental stages of plants (table 2; Harlan, 1992). The same traits appear to recur in widely different crops, providing additional evidence that they are the result of selection during domestication. Hence, this suite of diagnostic traits has been called the domestication syndrome. Fully domesticated plants, such as maize, beans, wheat, cotton, peas, and soybeans, possess the full array of traits included in the domestication syndrome. Partially domesticated crops such as oilseed rape and fruit trees possess only part of these traits. For example, the seeds of oilseed rape are still shed (in part) at maturity and exhibit some dormancy. Fruit trees are generally thought to have undergone limited domestication, often restricted to fruit characteristics such as size, color, and fleshiness.

Selection pressure or developmental stage	Specific trait
Increased harvest	Reduction or elimination of seed dispersal
	Changes in inflorescence morphology (e.g., more flowers)
	More synchronous flowering (e.g., reduced branching, shorter branches)
Increased seedling vigor	Larger seeds
	Nondormant seeds
Reproductive system	Day length insensitivity
	More reliable seed set (e.g., outcrossing to selfing)
Human selection	More colorful, different shapes, larger size (e.g., numerous crop examples)
	Reduction in toxic or unpleasant compounds
	Different uses (e.g., rice: glutinous vs. nonglutinous, long-grained vs. short-grained, aromatic)

***Source*: Modified from Harlan, 1992.**

Table 2. Traits selected during domestication of plants.

Types of Evidence Used to Study Crop Evolution

The study of the origin of domestication and evolution of crop plants and animal breeds is truly a multidisciplinary field. Initially, it was the Swiss botanist Alphonse de Candolle (1882), the father of biogeography, who suggested that four types of evidence could be used to trace back a crop to its center of domestication. The two most reliable types are botanical or zoological data and archaeological data. Botanical data consist of the area of distribution of the wild progenitor of the crop or the domesticated animal. Archaeological data include ancient remains of plants, such as seeds, identified in archaeological sites, such as temples and palaces of the antiquity. Additional data are historical or prehistorical documents or representations of crops or farm animals. Among these are herbals of the 15th century, Roman texts and a cookbook, cuneiform tablets, coins, and architectural ornaments. Linguistic evidence, such as words to designate a crop or its products, also provide evidence for the antiquity of cultivation.

Since Candolle's time, science has provided several additional tools (Harlan & de Wet, 1973; Smith, 1995). Data on the origin of domestication now include information from plants or animals on the one hand, and humans on the other hand. In both cases, both extant and ancient populations are studied (table 3). Some of the most recent evidence uses DNA sequences or markers to trace the origin of crops (e.g., common bean: Kami, Becerra,Velásquez, Debouck, & Gepts, 1995; maize: Matsuoka, Vigouroux, Goodman, Sanchez, Buckler, & Doebley, 2002; einkorn wheat: Heun et al., 1997). There is an increasing focus on the use of microscopic remains such as phytoliths (silica concretions taking on the shape of a plant cell in which they are contained) and starch grains (Piperno, Ranere, Holst, & Hansell, 2000; Piperno, Holst, Wessel-Beaver, & Andres, 2002). These microscopic remains have allowed

Plants or animals	Humans
Living	
Experimental taxonomy	Language
Geographic distribution	Oral tradition, creation beliefs
Ecological distribution	Techniques of cultivation, cooking
Genetic systems	Attitudes toward the crop, animal
Variation patterns	Nutritional effect on physical characteristics
Morphology, physiology	
Genetic reconstruction	
Ancient	
Archaeobotany or -zoology	History
Palynology	Art
Paleobotany	Archaeology
	Physical anthropology

***Source*: Modified from Harlan & de Wet, 1973.**

Table 3. Types of evidence used in the analysis of the origin of domestication of crop plants and animal breeds.

archaeobotanists to extend their investigations into hot and humid areas that are not as conducive to the conservation of macroscopic remains, such as seeds or fruits.

Domestication and Crop Evolution as Illustration of Evolutionary Processes

Domestication of plants and animals has a number of useful features as an experimental system to study and illustrate evolution:

1. The contrasting phenotypes distinguishing wild and domesticated phenotypes provide an excellent opportunity to make comparative observations on the development of plants (figure 1) and behavior of animals (although the latter is probably more difficult). Seeds of wild and domesticated types can be obtained from gene banks of the USDA (http://www.ars-grin.gov/npgs/searchgrin.html). Observations include those on seed size, shape, and color; and growth habit (number of branches, stem length between successive leaves, the number of days to flowering and to maturity, fruit size, etc).

2. Differences between wild and domesticated types also reflect different responses to environmental conditions. For example, the timing of maturity in some plants is set by the length of the day (or more accurately, the length of the night, also called the photoperiod). Plants that originate in temperate regions (e.g., *Arabidopsis thaliana*) generally flower under long days (e.g., 15–16 hours), whereas plants that originate in tropical regions flower under short days (11–12 hours). Dispersal of domesticated plants from their centers of domestication often involved adaptation to days of different length during the growing season, often achieved by selection for indifference to the length of the day. This can be illustrated by initiating simple experiments that modify the length of the day and observing the effect on flowering time.

3. Another advantage of the domestication process as a study system is that the wild progenitors of domesticated plants and animals in many cases still exist and can be observed in their native habitats. It has now been well established that agriculture started in a limited number of locations, broadly situated between 30° N and S latitude (figure 2). Although in many cases, these habitats are severely threatened by human pressure, such as overgrazing and conversion of natural to agricultural ecosystems, it still possible to observe the wild progenitors of plants and animals in these centers. Figure 2 provides some examples of crops domesticated in these different centers.

Figure 1. Examples of morphological traits in domesticated plants (D) and their wild progenitors (W). (a) ear of teosinte, the progenitor of maize (the Mexican 5 pesos coin is about the size of a U.S. quarter); (b) ear of maize; (c) pod of beans: at left, shattering pods of a wild bean; at right, tightly closed pods of snap bean; in the center, wild x domesticated hybrid; (d) shattering ear of teosinte; (e) fruit of wild squash (see arrow); (f) fruits of domesticated squash. (Photos: P. Gepts)

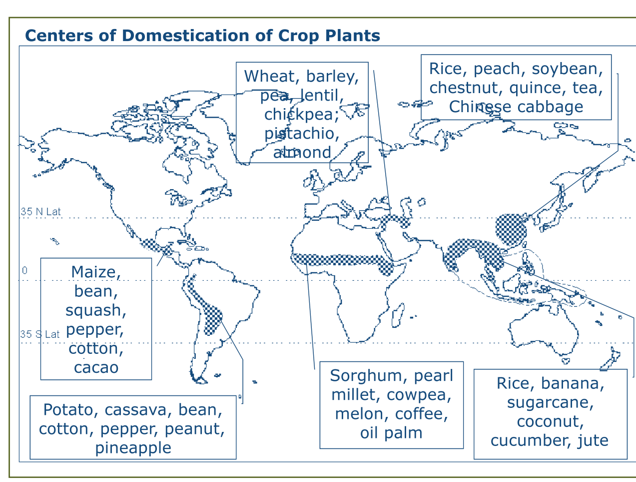

Figure 2. Major centers of domestication of crops. (From Gepts 2002, 2003).

4. Compared with evolution under natural conditions, evolution under anthropic conditions has acted fairly quickly. In general, the earliest crops were domesticated at about the same time in the different centers of agricultural origins some 10,000 years ago. The simultaneity of domestication in these far-flung centers is thought to be related to global warming following the last ice age. However, the specific scenario remains to be determined. It is generally thought that domestication may have taken some 1,000 years, although selection by humans has continued to this day and will continue in the future (Gepts, 2004a). Genetically, domestication could be achieved in considerably less that 1,000 years (Hillman & Davies, 1999), provided sufficient genetic variation, selection, and recombination are present. This observation suggests that major biological changes can be achieved over evolutionarily very short time periods.

5. The use of DNA marker technologies such as molecular linkage mapping and quantitative trait locus mapping have allowed us to locate the genes responsible for the morphological and physiological differences between wild and domesticated types, especially in plants. These studies, summarized by Gepts (2004a), have generally shown that some genes can have a major effect on the phenotype and that genetic effects predominate over environmental effects. Such a strong genetic control is consistent with a strong selection pressure operating during domestication. Further evidence for strong selection pressure has come from DNA sequence analysis of domestication genes in maize (e.g., Wang, Stec, Hey, Lukens, & Doebley, 1999, 2001).

6. One of the most generalized features of plant and animal domestication is the reduction in genetic diversity that has generally operated, regardless of the species involved. This genetic bottleneck has resulted from selection and genetic drift operating at various stages during the evolution of crops, including domestication itself, dispersal of the crop or animal by humans from the center of domestication, and modern breeding in response to specific market demands. An elegant example of the reduction in genetic diversity during archaeological times is provided by Jaenicke-Despres et al. (2003). They analyzed the sequences of three genes, presumably related to domestication of maize, in both archaeological remains of maize and contemporary populations of maize and its wild progenitor, teosinte. For two of the three genes, the diversity of alleles found in the wild progenitor had been lost some 2,700 years ago. Thus, the selection and manipulation of seed stocks by early farmers had had a fairly drastic effect on genetic diversity of the maize crop.

7. Although wild and domesticated types are quite distinct morphologically, physiologically, and behaviorally, they remain generally members of the same biological species. In general, they can intermate freely and give rise to viable and fertile progeny (Ellstrand, Prentice, & Hancock, 1999; Ellstrand, 2003). Thus, gene flow can occur between wild and domesticated types leading to the appearance of feral or intermediate types (Jarvis & Hodgkin, 1999).

Why Do Crop and Domestic Animal Evolution Matter?

Information about the origin of domesticated plants and animals and the effect of evolution under human cultivation and rearing has important consequences in a number of areas:

1. In plant and animal breeding, information about centers of domestication guides breeders to additional sources of genetic diversity. Indeed, centers of domestication are often also centers of genetic diversity for crops and domestic animals. Genetic diversity for traits such as resistance to diseases and pests, higher yield, and better nutritional traits are the raw material necessary to develop improved crop cultivars or animal breeds. Information, such as that presented in figure 2, is therefore essential to developing successful breeding programs. It helps guide crop and animal biodiversity conservation programs (Gepts, 1995; Bretting & Duvick, 1997; Maxted et al., 1997).

2. Although the focus of this chapter has been on plants and animals, geographic patterns of genetic diversity in associated organisms should also be

considered. Centers of origin and genetic diversity of the host organisms (animals or plants) are often also centers of origin of pathogens and pests, and their predators, as well as useful organisms, such as symbionts. Thus, information on the geographic distribution of genetic diversity in both host and associated organisms helps breeders identify more easily sources of resistance genes. An example of this approach is the common bean *(Phaseolus vulgaris),* which consists of two major geographic gene pools, Andean and Mesoamerican (Gepts, 1998). Several pathogens and one symbiont show the same geographic pattern of genetic diversity (e.g., Gepts & Bliss, 1985; Guzmán et al., 1995; Aguilar, Riva, & Peltzer, 2004). The genomics basis for differential resistance against strains of different gene pools resides in the diversification on ancestral gene clusters (Geffroy et al., 1999, 2000).

3. Membership in the same biological species results in the appearance of viable and fertile progeny in crosses involving wild and domesticated types. In some cases, these hybrids are benign and disappear. In others, they lead to the formation of problematic weeds, which are difficult to control because of their high similarity with the crop or domestic animal. It has been estimated that crop-to-wild gene flow has led to the formation of aggressive weeds in seven out of the 13 most important crops. Examples include rice and sorghum.

4. Few crops have been domesticated in areas that are now part of technologically advanced countries, such as the United States, the European Union, and Japan. In contrast, most crops have been domesticated in areas now occupied by third world countries. This geographic disjunction sets the stage for a classic conflict between the technology-rich North and resource-rich South (Gepts, 2004b). International treaties, such as the Convention on Biological Diversity (CBD: http://www.biodiv.org/default.shtml) and the trade-related aspects of intellectual property rights component (TRIPS) of the World Trade Organization (http://www.wto.org/english/tratop_e/trips_e/trips_e.htm), seek to develop a framework for transfer of technology in exchange for biodiversity. Currently, the situation is still unsettled. The United States has not ratified the CBD. Other countries have become loath to share their biodiversity with an important exception, the International Treaty on Plant Genetic Resources for Food and Agriculture (http://www.fao.org/ag/cgrfa/itpgr.htm), which is a multilateral treaty to freely exchange crops among signatory countries (Gepts, 2004b).

5. The small number of crops and animal breeds that have been domesticated suggests that it might be possible to domesticate additional ones for specific human uses. The last centuries have seen some partial domestications, mainly plantation crops such as the rubber tree *(Hevea brasiliensis)* and the African oil palm *(Elaeis guineensis),* and the silver fox in the former Soviet Union. The relatively simple genetic control of domestication should encourage scientists to pursue more domestications to fulfill unfilled human needs. Examples of these needs include plants that contain pharmaceutical compounds, either naturally or by genetic engineering. In planta production is potentially cheaper and can possibly deliver larger quantities of a high-quality, uncontaminated product. Currently, about one-quarter of medicines are derived from plants (Winslow & Kroll, 1998). Domesticating the plants from which these medicines are derived can potentially increase yields of the compounds and protect natural populations of these plants. Increasingly, plants are being genetically engineered to produce pharmaceutical (and industrial) compounds. For short-term practical reasons, the plants chosen are food crops such as maize, soybeans, and rice (Goldstein & Thomas, 2004), creating a potential contamination risk for the food chain. Domestication of additional plants for nonfood uses could provide more opportunities for pharmaceutical and industrial production (Andow, Daniell, Gepts, Lamkey, Nafziger, & Strayer, 2004).

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